

**REPRODUCTION OF SHORTNOSE STURGEON IN THE GULF OF MAINE:
A MODELING AND ACOUSTIC TELEMETRY APPROACH**

By

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Thesis Advisor: Dr. Gayle Zydlewski

An Abstract of the Thesis Presented
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The Penobscot River is the subject of an intensive river restoration project involving the removal of the two lowermost dams at river kilometers (rkm) 46 and 58. A third dam, Bangor Dam (rkm 41), was previously removed; however, portions of the structure remain in the river. This study investigated the extent of suitable spawning habitat for shortnose sturgeon downstream of the lowermost dam and the legacy effects of the Bangor Dam in relation to spawning migrations. A two dimensional hydrodynamic model was created and analyzed for spawning habitat suitability and passage at the dam using River 2D version 0.95a. Results indicate that suitable spawning habitat is present in the river reach accessible to shortnose sturgeon and they should be capable of passing the remnants of the Bangor Dam during spring river conditions. Although, passage above than Bangor Dam has not yet been observed in the spring and shortnose sturgeon with acoustic tags have not been detected above the Bangor Dam

remnants in the spring. The importance of upstream spawning migrations of shortnose sturgeon cannot be understated, and passage at the Bangor Dam remnants requires empirical study at spring discharges to further assess the probability of a water velocity barrier.

Shortnose sturgeon (*Acipenser brevirostrum*) of the Penobscot River were also monitored using acoustic telemetry. Telemetry results indicate a high rate of movement out of the Penobscot and exchange between the Penobscot and Kennebec Rivers. Most telemetered females with eggs in the late stage of development that overwintered in the Penobscot left the river system prior to suitable spawning conditions. No upstream movements were detected during presumed favorable spawning conditions and 922 hours of sampling failed to capture shortnose sturgeon eggs or larvae in the Penobscot River. Females with late stage eggs were later detected at known spawning areas in the Kennebec complex (Kennebec, Androscoggin, and Sheepscot Rivers). These results indicate that currently the Penobscot is unlikely to host spawning and suggest a metapopulation or patchy population structure within the Gulf of Maine.

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CHAPTER 1

APPLICATION OF HYDRODYNAMIC MODELING TO SHORTNOSE STURGEON (*ACIPENSER BREVIROSTRUM*) SPAWNING HABITAT AND PASSAGE IN THE PENOBSCOT RIVER, ME

1.1 Abstract

The Penobscot River is the subject of an intensive river restoration project involving the removal of the two lowermost dams at river kilometers (rkm) 46 and 58. A third dam, Bangor Dam (rkm 41), was previously removed; however, portions of the structure remain in the river. This study investigated the extent of suitable spawning habitat for shortnose sturgeon downstream of the lowermost dam and the legacy effects of the Bangor Dam in relation to their spawning migrations. A two dimensional hydrodynamic model was created and analyzed for spawning habitat suitability and passage at the dam using River 2D version 0.95a. Results indicate that suitable spawning habitat is present in the reach accessible to shortnose sturgeon (weighted usable area ranged from 21 – 44%) and they should be capable of passing the remnants of the Bangor Dam during spring river conditions (percent passable area ranged from 13-90% depending on tidal stage and river discharge). River conditions were assessed at five discharge levels as well as at low, mid, and high tidal stages for each discharge. Increasing river discharge resulted in less spawning habitat available and more spawning habitat is available at high tide than low tide. Similarly, passage at Bangor Dam was better at high tide and low discharge. The importance of shortnose sturgeon upstream

spawning migrations cannot be understated, and passage at the Bangor Dam remnants requires empirical study at spring discharges to further assess the probability of a water velocity barrier.

1.2 Introduction

Within the United States, dam removal is becoming a viable option for ecologically restoring impounded rivers (Babbitt 2002). Dam removals lead to the restoration of natural hydrologic flow regimes, restore natural sediment transport, and allow migratory fish species access to additional habitat (Bednarek 2001). High costs associated with purchasing, decommissioning, and removing dams have resulted in a lack of scientific studies pre and post dam removal (Babbitt 2002). An example of a lost opportunity to assess ecological responses to a dam removal occurred when, in the early 1980's, the Federal Energy Regulatory Commission refused to relicense the deteriorating Bangor Dam. This dam was consequently removed; however, portions of the structure remained in the river (Opperman 2011) and responses of anadromous fish to the removal is unknown, as scientific data and even anecdotal evidence are lacking.

The Penobscot River is again poised for restoration activities (via dam removal). The two current lowermost dams on the Penobscot River, Veazie Dam (rkm 46, situated at head of tide) and Great Works Dam (rkm 58), will be removed by 2015 (Figure 1.1). This is expected to restore habitat and habitat access for anadromous fish populations. Access to habitat for diadromous species such as Atlantic salmon (*Salmo salar*) is expected to increase to approximately two thirds of historic habitat (Opperman 2011). Unlike Atlantic salmon, shortnose sturgeon habitat in the Penobscot River prior to dam

construction was likely limited by high water velocities at the natural falls that were present at the site of the Milford Dam (rkm 62), which will remain in place. In addition, Gillman Falls on the Stillwater River probably restricted shortnose sturgeon habitat as well. Following the removals of Veazie Dam and Great Works Dam, shortnose sturgeon should have access to nearly 100% of their historic range in the mainstem Penobscot, excluding the Stillwater River which will remain dammed. This project is part of pre-removal research on the Penobscot River and focuses on quantifying suitable spawning habitat prior to removals, and assessing shortnose sturgeon passage at the site of the Bangor Dam remnants.

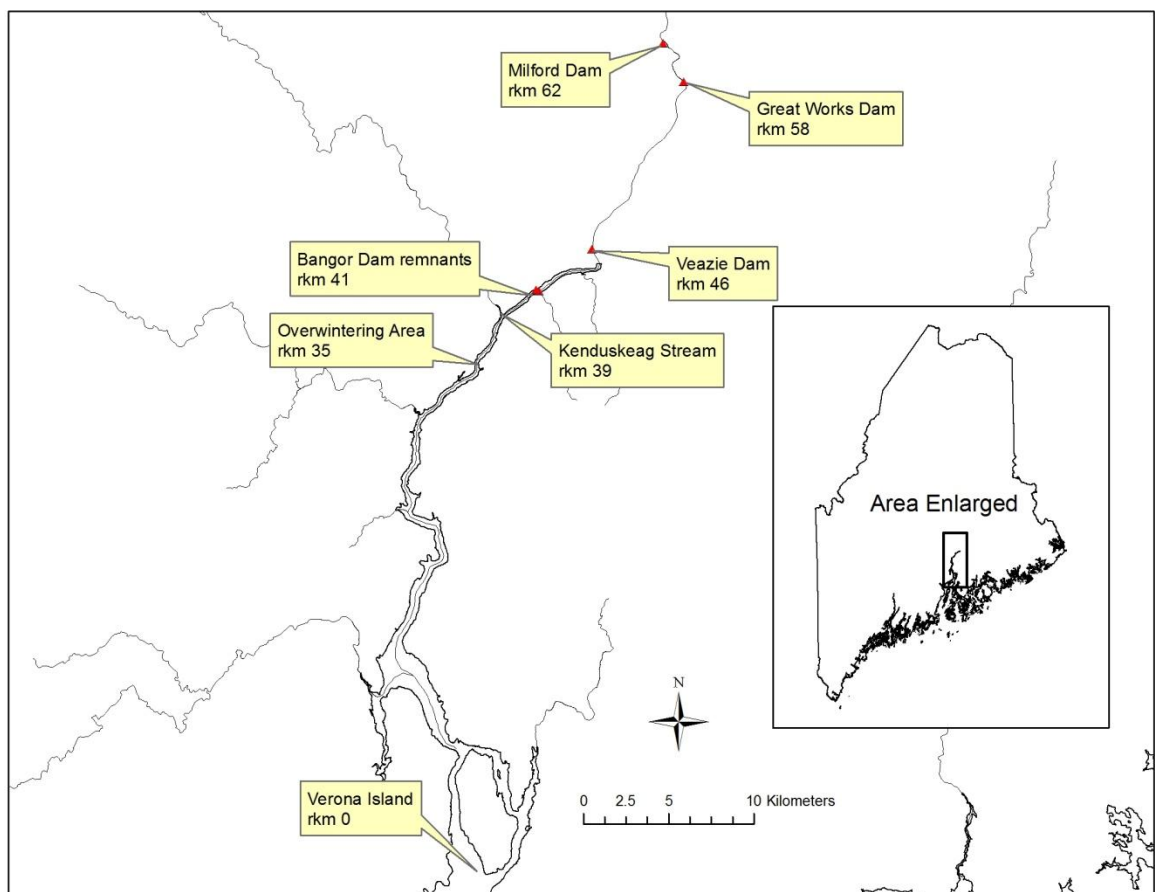


Figure 1.1. Study area. This study took place in the lower Penobscot River downstream of Veazie Dam (rkm 46).

Bangor Dam remnants remaining in the river may have a lasting legacy effect. These remnants form a narrow, shallow lip that spans the width of the river. The river bed deepens immediately upstream and downstream of these remnants, creating high water velocities. Acoustic telemetry has not documented a shortnose sturgeon passing above the Bangor Dam in the spring between 2007 and 2011. However, 50% of shortnose sturgeon with acoustic tags have been detected passing above the Bangor remnants in the summer and fall at reduced discharges. For fish species that do not have exceptional swimming abilities, the Bangor remnants have the potential to limit upstream passage by creating un-passable water velocities at spring discharges. Relevant measures of sustained and burst swimming speeds are essential to determine threshold velocities for successful passage. Generally, sturgeon are not known to be exceptional swimmers; however, shortnose sturgeon swimming capability remains largely unstudied. Swimming performance of lake sturgeon (*Acipenser fulvescens*) is the closest studied analog to shortnose sturgeon. Peake et al. (1997) measured swimming speeds of five lake sturgeon, 106 – 132 cm total length. The size range of lake sturgeon in the study is a close approximation of reproductively mature shortnose sturgeon in the Penobscot River (Dionne et al. submitted) and may provide insight into passage and effects of the Bangor Dam remnants.

Shortnose sturgeon passage at the Bangor Dam remnants is an important consideration for river restoration in the Penobscot River. Upstream spawning migrations in the spring are a characteristic of shortnose sturgeon life history. In other impounded systems, shortnose sturgeon often spawn directly (within 500 m) below the first blockage to upstream migration (Duncan et al. 2004, Kynard 1997). In the

Penobscot River, shortnose regularly overwinter downstream of the Bangor Dam remnants and need to pass upstream to reach potential spawning habitat in the spring. Currently, this would be near the base of the Veazie Dam if sturgeon are capable of passing the Bangor Dam remnants. Also, shortnose sturgeon usually spawn when water temperatures are 9 – 15°C and bottom water velocities are 0.4 – 1.8 m/sec; over substrates of cobble, gravel, boulder, and ledge (Kynard 1997, Dadswell et al. 1984).

Knowledge of such habitat preferences can be used to predict or identify potential, current, or future spawning habitat. Spatially-explicit, species-specific habitat models can and have been used to predict abundance, distribution, and preference of spawning sites for multiple species (Yamada et al. 2003, Yi et al. 2010). Habitat suitability index (HSI) models rely on rankings of various abiotic factors based on their suitability for different life stage needs (USFWS 1981). Suitability rankings range from zero to one, zero being completely unsuitable and one being completely suitable (USFWS 1981). Data incorporated into HSI's can be any variable an organism responds to, such as substrate type, water velocity, water depth, temperature, or food availability. Suitability curves, for multiple habitat variables can then be analyzed within a predictive model to identify potential “suitable” habitat within modeled reaches. This type of modeling can be applied to shortnose sturgeon since their spawning sites are linked to physical factors such as substrate, velocity, and depth.

Habitat factors characteristic of shortnose sturgeon spawning sites have been described in most known spawning areas (Dadswell et al. 1984). Crance (1986) compiled much of this information into HSI curves specifically for shortnose sturgeon spawning habitat. Habitat suitability curves developed by Crance (1986) are generalized

across the entire range of the shortnose sturgeon. As such, parameter values include data from northern and southern populations (Crance 1986). However, physical characteristics of spawning sites vary between northern and southern populations (Kynard 1997). As such, HSI parameters may need to be altered from Crance (1986) to accurately predict potential spawning habitat in northern or southern rivers prior to use in predictive models.

Habitat suitability index models can be used in conjunction with hydrodynamic models to provide robust habitat suitability estimates under existing or modified flow conditions (Steffler and Blackburn 2002, Tiffan et al. 2006). Hydrodynamic models can be developed for a variety of applications ranging from flood inundation to aquatic organism habitat simulations (Yi et al. 2010, Babaeyan-Koopaei et al. 2003, Wu and Mao 2007, Tiffan et al. 2006). However, to accurately model flow fields within a channel, hydrodynamic models need to be developed with detailed bathymetry (Crowder and Diplas 2000). In addition to predicting flow fields, habitat use and preference data can be used to predict suitable habitat within a modeled reach. Yi et al. (2010) incorporated observational data of abiotic factors, including depth, velocity, and substrate at known Chinese sturgeon (*Acipenser sinensis*) spawning sites into HSI curves. These HSI curves were used to predict, with a two-dimensional hydrodynamic model (River 2D), potential Chinese sturgeon spawning habitat at varying discharges below the Gezhouba Dam, China with the goal of recommending dam operations most likely to benefit Chinese sturgeon reproduction. Their study illustrates the use of predictive models to assess the impact of different management strategies on fish habitat.

In this context, it is imperative to determine which factors are most likely to improve recovery efforts, whether they are increasing habitat access, improving spawning habitat, or a combination of both. The potential of the Bangor remnants to restrict habitat access, for some species, long after its removal is an important consideration for the Penobscot River restoration upstream of that site. If a water velocity barrier at the Bangor Dam remnants is present, it could continue to impede spring spawning migrations of shortnose sturgeon. Consequently, the removal of Veazie Dam and Great Works Dam will have a limited impact on shortnose sturgeon if they are not able to pass the remnants during spring discharges. The goal of the present study was to assess the extent of spawning habitat suitability in the tidally influenced reach below Veazie Dam using River 2D and HSI curves, and to determine if a water velocity barrier is present at the Bangor Dam remnants.

1.3 Methods

1.3.1 Modeling framework

River 2D is a two-dimensional, depth averaged model that can be used specifically for fish habitat analyses (Steffler and Blackburn 2002). A River 2D hydrodynamic model is constructed in a series of steps. Bathymetry is first collected and then transformed into a digital elevation model. Nodes, located at the vertices of mesh elements, are then overlaid on the digital elevation model, and boundary conditions specified. Finally, the modeled domain is run to convergence; when inflow and outflow discharges are approximately equal. Water velocity and depth predicted by the model are based on bed elevation, the only measured input parameter. Once a model is calibrated,

suitable habitat can be predicted. Habitat suitability is calculated for each node in a modeled domain based on physical parameters, e.g., depth, velocity, or a combination of both (combined suitability). Each parameter is assigned a suitability value between zero and one. Depth and velocity suitability values are then used to calculate the amount of suitable habitat at each node; either based on depth, water velocity, or a combination of both. Different suitability curves can be developed to simulate and test other hypotheses based on depth and water velocity, such as passage.

Habitat analysis output, via River 2D, is also spatially referenced in the same coordinate system as the input bathymetry. Spatial output consists of geographically referenced model nodes, their depth and velocity suitability indices, and area of suitable habitat. Habitat suitability indices were used to address changes in habitat suitability at different discharges and different tidal stages (high, mid, and low). Additionally, passage at the Bangor Dam remnants was addressed with these tools.

1.3.2 Bathymetry Collection and Model Construction

Bathymetry was collected in 2008 (by Stantec Inc.) at low summer flows from Veazie Dam to 11.3 km downstream of the dam. These data were incorporated into a two-dimensional hydrodynamic model using University of Alberta's River 2D version 0.95a software. Bathymetric data used to construct the model was sparse in the Bangor Dam reach due to the complex features that were not adequately captured during the initial survey. To build a higher resolution model to address passage at the Bangor Dam, additional bathymetry was collected in 2011 and combined with the 2008 survey data (Figure 1.2).

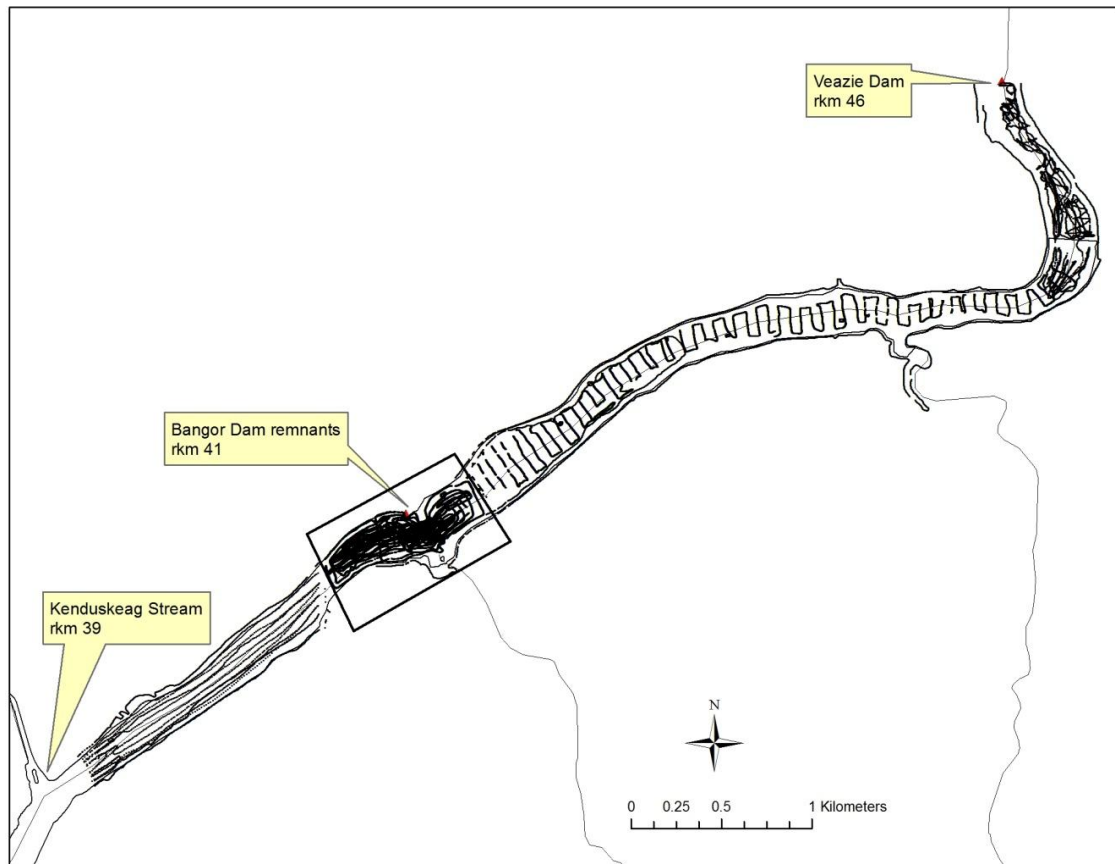


Figure 1.2. Map of combined 2008 and 2011 bathymetric survey data points. 2011 data points in the Bangor Dam reach are contained in the black box.

Bathymetry surveys in 2011 were conducted with a Teledyne RD Instruments Rio Grande 1200 kHz Acoustic Doppler Current Profiler (ADCP). All data were collected in real time with an on-board PC using Bathmapper 2.9.17 software (USGS 2012). The ADCP was mounted on the port gunwale and the instrument head was submerged to 0.2 m. A Garmin GPS 17HVS, mounted on a 2.0 m mast directly above the ADCP, was also connected to the PC to provide spatial information during data collection (accuracy < 3 m). Bathymetry was collected throughout the tidal cycle and a Bathmapper application was used to account for tidally influenced depth variation by stage, correcting bathymetric data to high tide based on a USGS gauging station located 3 km downstream of the Bangor Dam remnants.

ArcGIS was used to compare bathymetry points collected in 2008 with 2011 data. Data points from 2008 were paired with 2011 data points if they were within 1.5 m of each other. Paired data points (n=25) differed significantly with a mean difference of -0.98 m (paired t-test: $t=-6.862$, $df = 23$, $P<.001$) between the 2011 and 2008 data. Data from 2008 was corrected to 2011 bathymetry using the mean difference between paired data points of -0.98 m. Only data from the comprehensive 2011 survey was used for the detailed assessment of flows in the vicinity of the Bangor Dam site. Data collected in 2008 was removed from the dataset in the Bangor Dam reach and downstream of the Kenduskeag Stream confluence. All remaining 2008 data, corrected to 2011 stages, was combined with the 2011 dataset to provide a dataset with increased spatial coverage and resolution.

These bathymetric data were used to generate a digital elevation model in River 2D Bed. River 2D's mesh generation program was then used to create the computational mesh utilized for the hydrodynamic simulation by overlaying nodes on the digital elevation model. Nodes were placed in the entire domain on a 20 m grid, and node spacing was reduced to 10 m in the Bangor Dam reach. The entire domain was refined based on large elevation difference elements, triangles containing an elevation difference greater than 0.5 m, and then smoothed. Finally, inflow and outflow boundaries were defined and a River 2D input file was created with an inflow of 315 cms to simulate discharge during ADCP validation surveys.

To validate depth and velocity data modeled with River 2D, depth and water velocity measurements were made with a Teledyne RD Instruments Rio Grande 1200 kHz ADCP. All data were collected in real time with an on-board PC using Teledyne

RDI WinRiverII software (Teledyne RD Instruments 2003). Again, a Garmin GPS 17HVS was also connected to the PC to provide spatial information for each sampling location. The ADCP and GPS were mounted as described above.

Depth and velocity measurements were taken in high turbulence areas which required special considerations while collecting data. The ADCP was programmed to record data at 0.2 s intervals in one-ping ensembles. A large number of one-ping ensembles ($n=600$) were collected at each measurement location in order to minimize error introduced by turbulence. These data were then post processed and all ensembles from an individual point were combined and averaged; this resulted in one depth measurement and a depth averaged velocity measurement at that point.

Collection of approximately 600 ensembles per location ($n = 33$, with approximately 15 m spacing) required four to five minutes of data collection at each sampling point. Due to the length of time needed to collect data at each location, the boat was double anchored to minimize lateral movement to approximately one square meter. This movement was considered acceptable, as bathymetry was collected on a 2 m^2 grid and the model developed with a minimum grid size of 10 m^2 . Field measurements were collected on October 12 ($n=24$) and December 7, 2011 ($n=9$) at river discharges of 283 cubic meters per second (cms) and 294 cms respectively (Figure 1.3). Data were collected October 12 at the Bangor Dam remnants and December 7, 1.9 km downstream of the remnants. Discharge data was obtained from a USGS gauging station (rkm 101) at West Enfield, ME. All points were collected during the first two hours of the outgoing tide.

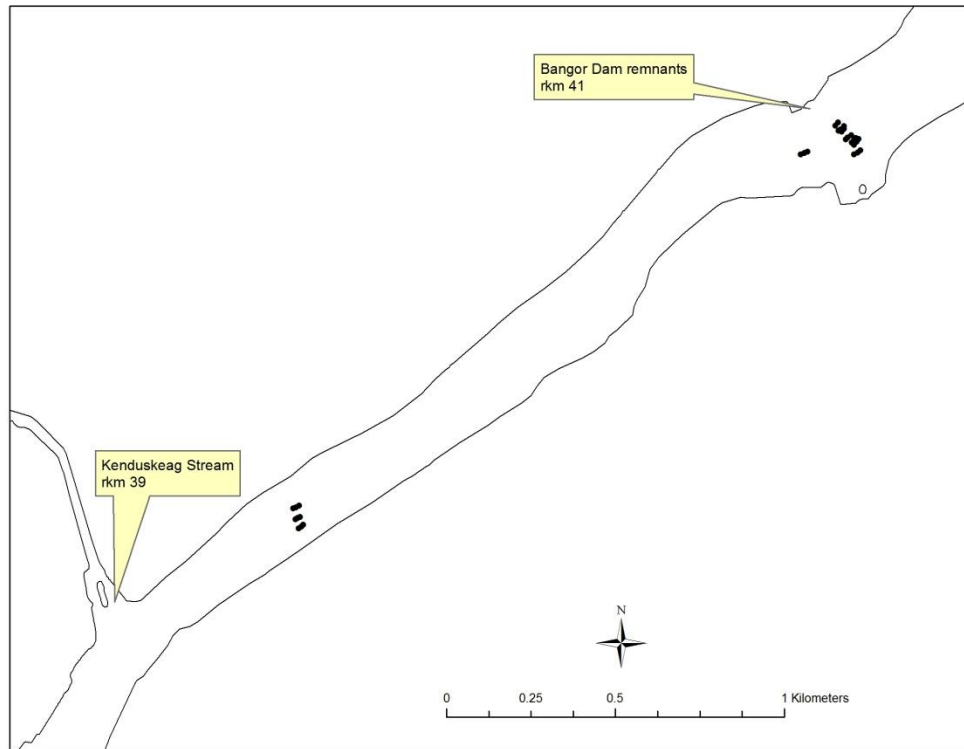


Figure 1.3. Locations of ADCP depth and velocity validation points. These points were collected in the modeled reach between Veazie Dam and the confluence of Kenduskeag Stream.

1.3.3 Depth Validation and Calibration

Initial validation was restricted to the full reach model, Veazie Dam (rkm 46) to Kenduskeag Stream (rkm 39), developed at a river discharge of 315 cms. The model was created at a higher discharge value than reported discharge (283 cms) at West Enfield during data collection to account for eight tributaries between the gauging station and the modeled reach. To validate depth within these models, each ADCP field measurement was referenced to an individual model node using ArcGIS. Prior to comparison, field measurements were stage corrected to high tide using gauge height data from a USGS gauging station site at the confluence of Kenduskeag Stream and the Penobscot River (rkm 39). Once corrected to high tide, field measurements were adjusted for mid and low

tidal stages by subtracting the observed tidal range (low tide stage), and subtracting half of the observed tidal range (mid tide stage). Stage correction allowed field measurements to be compared directly to predicted depths at a given tidal stage.

Initial calibration was conducted on the 315 cms high tide model and progressed to mid and low tide models successively. The 315 cms model was initially run with an arbitrary downstream boundary elevation of four meters. Once the model converged to a stable solution, nodal depth values were exported. Predicted depth values were compared to stage corrected field measurements with a paired t-test. If the paired t-test indicated that the values from the model and observed values were significantly different ($p\text{-value} < 0.05$), the difference was quantified. Models were calibrated by changing the downstream boundary elevation by the mean depth difference, provided by the paired t-test, between the observed and predicted depth values. The model was then run again and analyzed in the same manner until predicted depths were consistent with stage corrected values. Calibration of the mid tide model began by determining the tidal range on days when discharge was within 10 cms of validation discharge ($n=6$) and then using half that difference to estimate the mid tide height. The difference in gauge height between high and mid tides was subtracted from all ADCP stage corrected field measurements. The downstream boundary condition was reduced by the same amount to simulate the water elevation of mid tide. Calibration procedures were the same procedures used for the high and low tide models.

1.3.4 Velocity Validation

Velocity validation was completed following depth calibration. Once the 315 cms models were calibrated for depth, nodal velocity values were exported and compared to field measurements with paired t-tests. Velocity data could not be stage corrected because field measurements were only collected during the first 2.5 hours of the ebb tide. As such, observed and predicted water velocities were only compared for high and mid tide models. Validation points were only included if they were collected within one hour of the selected tidal stage.

1.3.5 Spring Model Calibration

Hydrodynamic models of spring conditions (spring discharge models) were developed by assessing discharge and temperature data from April 1 to June 7 of 2003 - 2007 from USGS gauging stations at Eddington Bend (rkm 45) and West Enfield (rkm 101). Archived data from the gauging station at Eddington Bend contained water temperature data while the West Enfield gauging station archive contained discharge data. Data were selected from each station and combined in a temperature and discharge dataset. A subset of discharge data (during periods of increasing water temperature and decreasing discharge consistent with the shortnose sturgeon spawning window (Kynard 1997) was then divided into percentiles. Selected model discharges were the 5th, 25th, 50th, 75th, and 95th percentiles of compiled discharges for the 2003-2007 period to characterize spring river conditions (Figure 1.4). Discharge values were adjusted due to the distance and number of tributaries (n=8) between the West Enfield and Eddington Bend gauging stations. The magnitude of the adjustment (198 cms) was determined with

the modified rational equation to determine peak discharge within all tributary basins (Arnold et al. 1998).

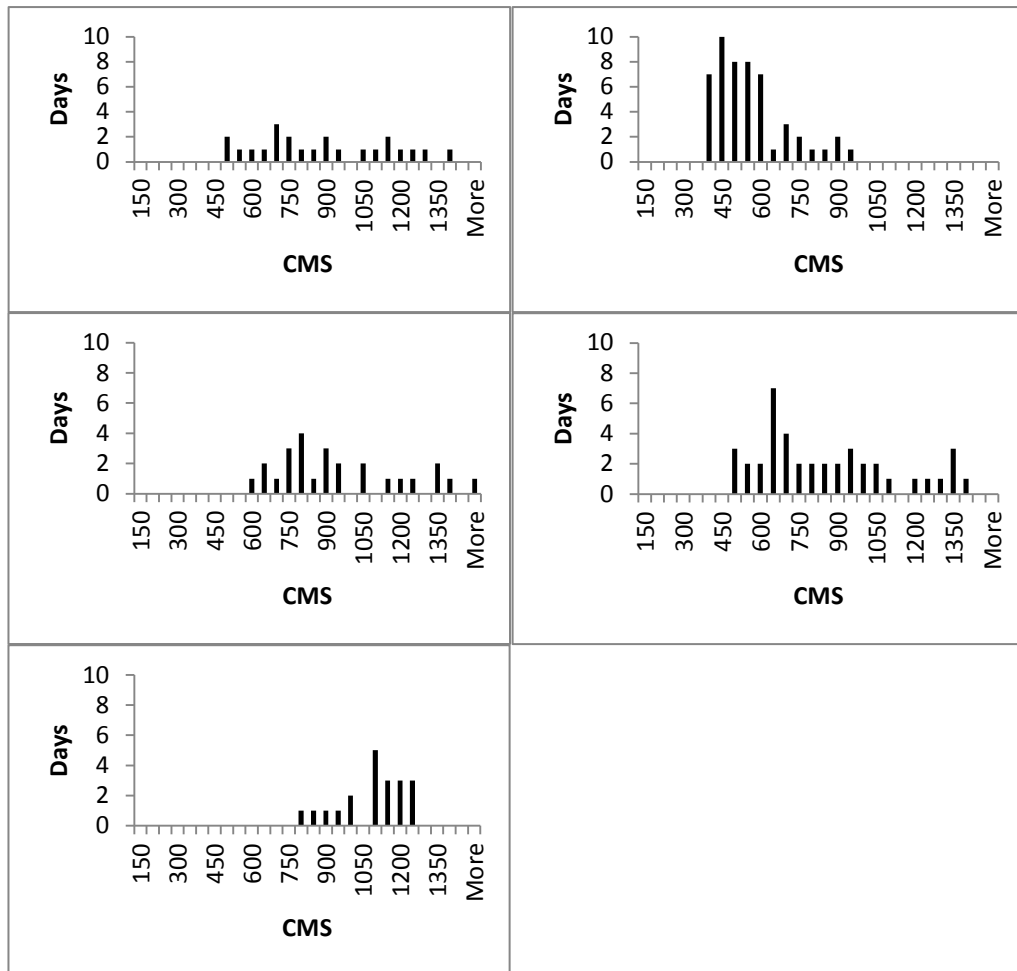


Figure 1.4. Spring discharge histograms. Histograms of discharge (in cubic meters per second, cms) during the spring spawning window 2003-2007. Panels show individual years and progress right to left from 2003 at the top to 2007 at the bottom.

Spring discharge models (412 cms, 580 cms, 793 cms, 1009 cms, and 1308 cms) incorporated tidal range data from the USGS gauging station at Bangor, ME (rkm 39). Maximum and minimum gauge height data were averaged over all days of record that discharge was within 10 cms of selected levels. The difference between maximum gauge height on December 7, 2011 and average maximum gauge height of selected discharge

was added to the downstream boundary of the high tide 315 cms model. Discharge at the inflow boundary was changed to the selected spring flow and the model was run to convergence. Prior to analysis, ADCP field measured depths were adjusted to the average gauge height of selected discharge and tidal stage. Predicted depth values were exported from the model and compared with observed depths with a paired t-test. If depth values were significantly different ($p\text{-value} < 0.05$) the downstream boundary condition was adjusted. The model was re-run until predicted and observed depths were not significantly different across all sites, but does not account for spatial bias (Figure 1.5). This procedure was used for all spring flow discharge levels and tidal stages.

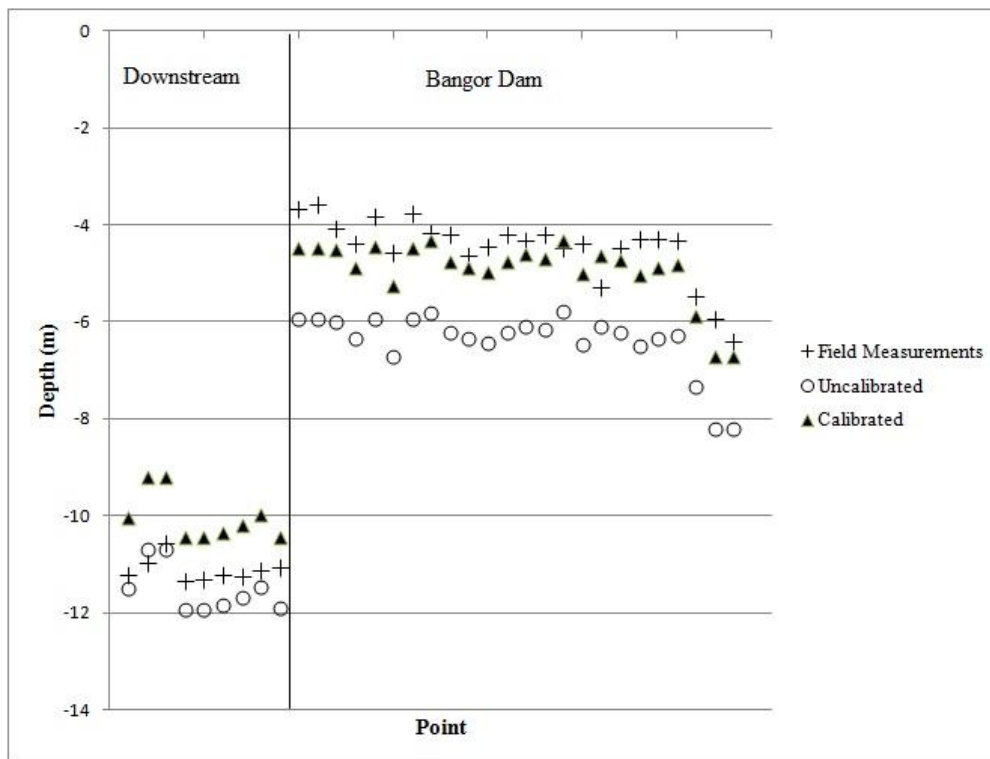


Figure 1.5. Difference between un-calibrated and calibrated model depths. The mean difference between water depths of the pre-calibrated model and field measurements was used to adjust the downstream boundary to calibrate the model. This example is from the 793 cms high tide model.

1.3.6 Spawning Habitat Analysis

Spawning habitat suitability was assessed at all discharges and tidal stages following the calibration of all models. Spawning habitat suitability for each model was calculated based on HSI curves by Crance (1986) and modified using data from Kynard (1997) (Figure 1.6). Spawning habitat suitability was calculated for each River 2D flow model and the following data exported for analysis: depth, velocity, velocity suitability, depth suitability, combined suitability, and weighted usable area (WUA).

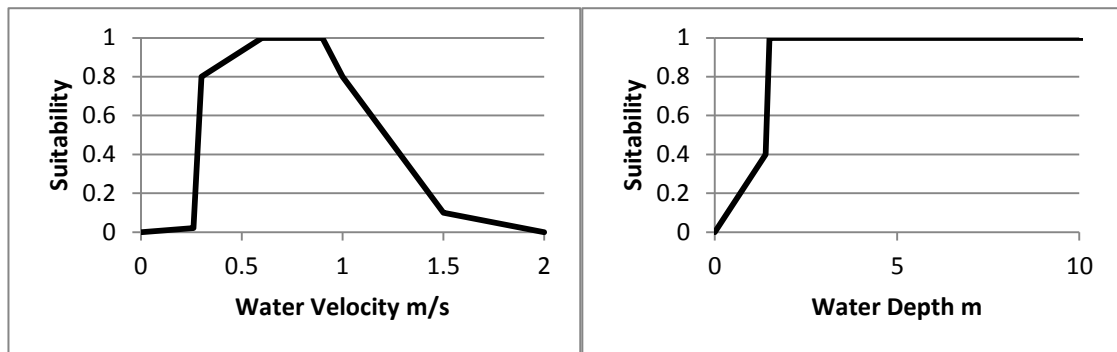


Figure 1.6. Spawning habitat suitability index curves. These curves were used for estimation of suitable spawning habitat within River 2D. Both curves were modified from Crance (1986) based on Kynard (1997).

Combined suitability was calculated using the minimum method in River 2D, which uses the smaller suitability value whether it is depth or velocity (Steffler and Blackburn 2002). The combined suitability value was then used to calculate the spatial area associated with the node that was suitable for spawning. This was the WUA of an individual node. The sum of all nodal WUA's (total WUA) in the domain was also calculated. Percent WUA was calculated by dividing the total WUA by the total area of the modeled domain. Percent WUA was used to compare spawning suitability among the models due to differences caused by tidal fluctuations and discharge levels. This method

was used to assess patterns in suitable spawning habitat for both the full reach and also the reach 1.0 km downstream from Veazie Dam.

Spawning suitability was also assessed graphically. Images of spawning suitability were exported and compared for each spring discharge and stage to determine if areas below Veazie Dam were predicted to be suitable in the majority of simulations. While not easily quantified, the visual comparison provides insight concerning probable spawning locations.

1.3.7 Passage Analysis

High water velocities were observed at the bathymetric feature at the Bangor Dam remnants during spring runoff. River 2D was used to conduct a passage analysis on a cross section of the river directly over the remnants. For each spring discharge (412 cms, 580 cms, 793 cms, 1009 cms, and 1308 cms) and tidal stage (high, mid, and low), passage was assessed with two different HSI curves representing the swimming performance of adult shortnose sturgeon. Lake sturgeon, with total lengths ranging from 106 – 132 cm, sustained a maximum speed of 0.83 - 0.97 m/s and swam for short periods at speeds of 1.8 m/s (Peake et al. 1997). To account for possible differences in swimming performance between species, HSI water velocity parameters were altered to represent two different swimming performances: 1 m/s and 2 m/s (Figure 1.7). The 1 m/s HSI allows un-impeded passage between water velocities of 0.0 m/s and 1.0 m/s, passage suitability then declines linearly to zero at a water velocity of 2 m/s. Both passage HSI curves were constructed in this manner with respect to water velocity. The depth parameter in both HSI curves was set to allow unimpeded passage at all depths in excess

of 1.5 m based on the assumption of shortnose sturgeon avoiding shallow water during upstream migration. Suitability values and WUA's were calculated and nodal attributes exported for each model and HSI.

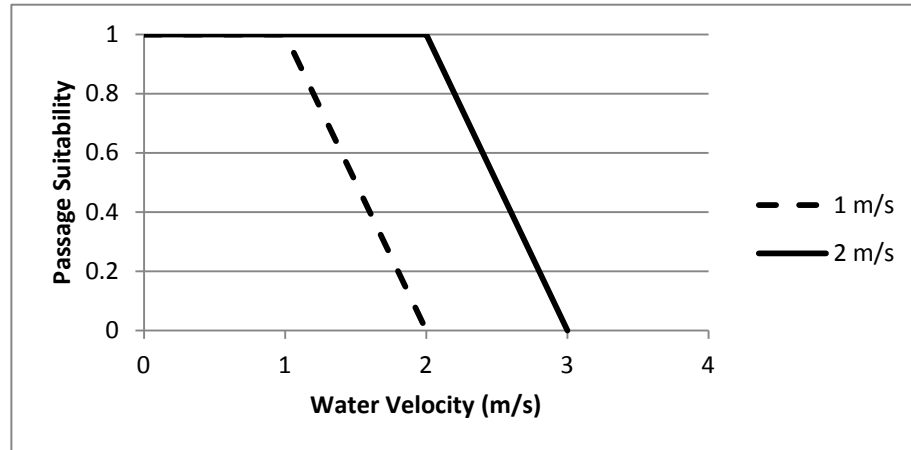


Figure 1.7. Passage suitability index curves. These curves represent the two shortnose sturgeon swimming performances used in the passage analysis.

Nodal attribute files were post-processed by selecting only nodes contained in the cross section at the Bangor Dam remnants. Passage over the entire cross section was assessed at each discharge and tidal stage by determining the average suitability index and also percent WUA within the cross section. Average suitability was calculated by taking the average of all nodal combined suitabilities. Percent WUA was calculated by summing nodal WUA values and dividing by the total area represented by those nodes. In addition, the selected nodes were also placed in four groups, each representing a quarter of the cross section from left to right. Percent WUA was calculated for each cross sectional quarter.

1.4 Results

1.4.1 Model Calibration and Validation

All models were derived from a single mesh. This mesh had a quality index of 0.12, slightly below the recommended quality index of 0.15 (Steffler and Blackburn 2002). Attempts to improve the mesh quality index to 0.15 were unsuccessful. All models, once converged, were calibrated and validated for high tide and mid tide, except for the 1009 cms mid-tide stage model and all 1308 cms models (Table 1.1). Low tidal stage models could not be accurately calibrated due to a hydraulic jump at the Bangor Dam remnants. This was also an issue with the 1009 cms and 1308 cms models. Paired t-tests revealed that all low tidal stage models could not be normalized to measured depths. Regardless of iteration, paired t-test results from all of these models determined that predicted and measured depth values were significantly different. Predicted depths in the Bangor Dam reach were deeper and predicted depths 1.9 km downstream were significantly shallower than measured values. This observation was consistent for all low tidal stage models.

Table 1.1. Depth calibration and validation paired t-tests. This table shows each discharge modeled in cubic meters per second (cms) and the results of paired t-tests between ADCP data points and points within the model with respect to water depth. Stage (high, mid, and low) and elevation are shown for each model ran and analyzed. The elevation is the height, in meters, of the downstream boundary elevation.

Model	Stage and Elevation	P-value	95% Confidence Interval	Mean Difference (m)
315cms	High 2.9	0.82	-0.30 , 0.24	-0.03
	Mid 1.3	0.29	-0.42 , 0.13	-0.15
	Low 0.1	< 0.001	-1.02 , -0.44	-0.73
412cms	High 2.9	0.73	-0.32 , 0.23	-0.05
	Mid 1.3	0.20	-0.46 , 0.10	-0.18
	Low 0.1	< 0.001	-1.11 , -0.50	-0.81
580cms	High 2.9	0.56	-0.36 , 0.20	-0.08
	Mid 1.3	0.09	-0.55 , 0.04	-0.26
	Low 0.1	< 0.001	-1.30 , -0.64	-0.97
793cms	High 2.9	0.34	-0.42 , 0.15	-0.13
	Mid 1.3	0.08	-0.59 , 0.03	-0.28
	Low 0.1	< 0.001	-1.38 , -0.63	-1.00
1009cms	High 2.9	0.17	-0.50 , 0.09	-0.20
	Mid 1.3	0.01	-0.76 , -0.09	-0.43
	Low -0.1	< 0.001	-1.63 , -0.79	-1.21
1308 cms	High 2.9	0.05	-0.63 , 0.00	-0.31
	Mid 1.3	0.001	-1.03 , -0.29	-0.66
	Low 0.1	< 0.001	-2.18 , -1.30	-1.74

Measured and predicted velocity validation values also differed significantly for the two 315 cms models (high and mid tidal stages) that could be compared to field data (Table 1.2). These two models consistently predicted slower water velocities than measured velocities. While measured and predicted values were significantly different, the mean error was not excessive. The mean velocity prediction difference for both models was 0.31 and 0.11 m/s respectively. In addition, bed roughness coefficients and eddy viscosity parameters were adjusted, but did not result in more accurate velocity

estimates. Because water velocity data were not available at spring model discharges, it was assumed that all other models underestimated water velocity as well.

Table 1.2. Velocity validation. Validation results of the high and mid 315cms paired t-tests.

Model	Stage and Elevation	P-value	95% Confidence Interval	Mean Difference (m/s)
315cms	High 2.9	<0.001	0.261 , 0.368	0.315
315cms	Mid 1.3	<0.001	0.072 , 0.160	0.116

1.4.2 Spawning Habitat Suitability

Predicted suitable spawning habitat exhibited the same spatial patterns with respect to tidal stage at every discharge level. Percent WUA was greatest in the high tide stage for each discharge and decreased with successive mid and low tide models (Table 1.3). Spatially, a small amount of suitable spawning habitat was distributed along the margins of the river from Veazie Dam to 3 km downstream. The majority of suitable habitat was distributed throughout the rest of the downstream reach (Figure 1.8). All spring discharge models exhibited the same spatial distribution of suitable spawning habitat.

Table 1.3. Percent suitable spawning habitat. Percent suitable habitat was calculated for the modeled domain from Veazie Dam to Kenduskeag Stream by dividing the amount of suitable spawning habitat (WUA) by the total area of the modeled domain. Discharge units are cms and tidal stages are high, mid, and low. Finally, the average of all percent suitable habitat was averaged for each model and is shown under "average."

Discharge	High	Mid	Low	Average
412	0.44	0.43	0.40	0.42
580	0.48	0.39	0.31	0.39
793	0.48	0.35	0.26	0.36
1009	0.43	0.28	0.23	0.31
1308	0.34	0.24	0.21	0.26

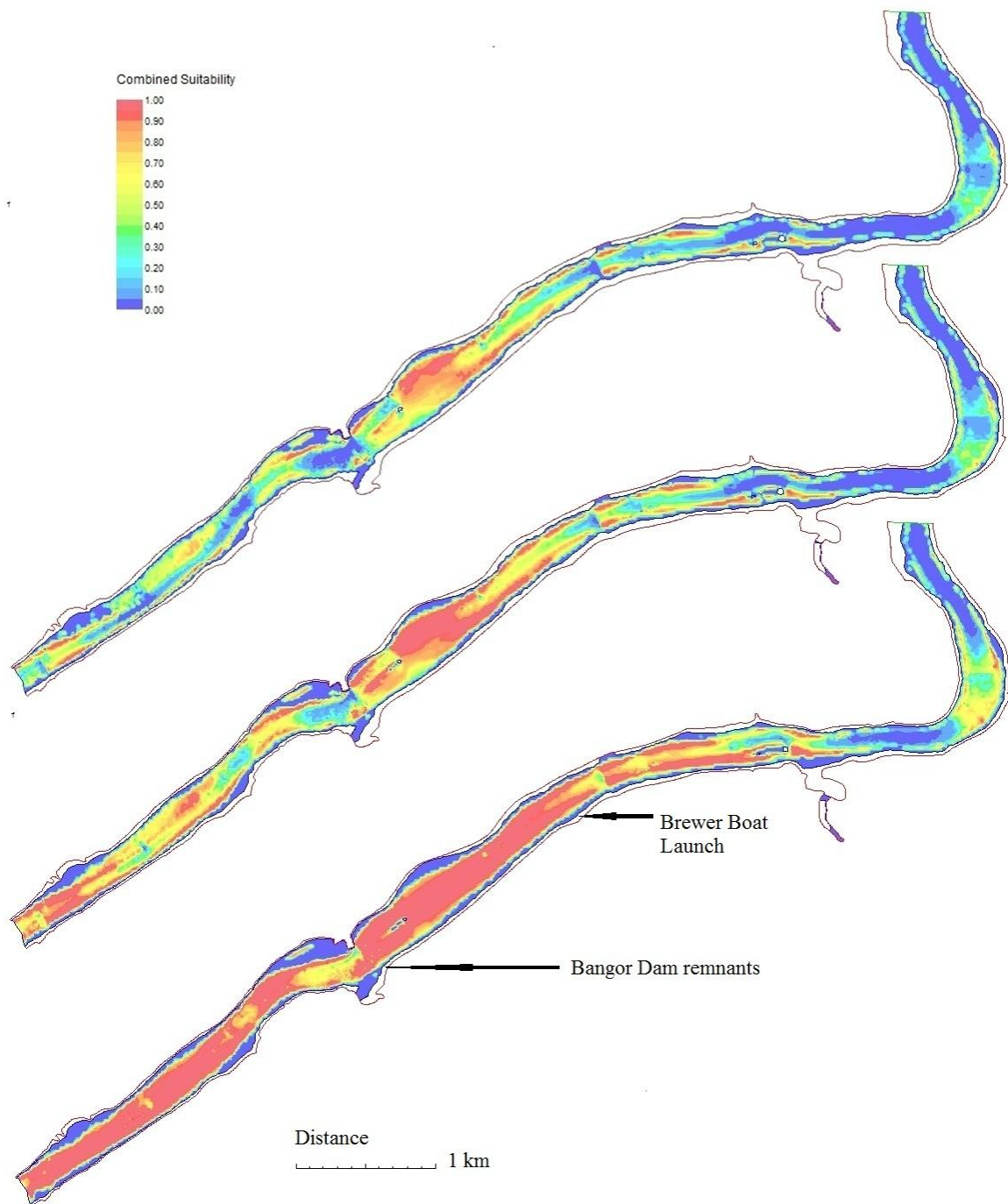


Figure 1.8. Spawning suitability of the modeled reach. These images show the predicted spatial distribution of predicted suitable spawning habitat at a discharge of 793 cms. Top model is low tide, middle model is mid tide, and bottom model is high tide. Note that the majority of the suitable habitat is greater than two kilometers from Veazie Dam. Areas of higher suitability are shown in warm colors.

Analysis of the first kilometer downstream of Veazie Dam (rkm 46-45) exhibited the same pattern as the entire modeled domain. For each discharge, the highest percent WUA occurred within the high tide model. However, the usable area in that kilometer was a much smaller percent of the total area than the percent WUA in the entire domain (Table 1.4). Spatially, suitable habitat was restricted to areas close to shore or behind large boulders or other obstacles. In addition, there were areas along the right and left bank a short distance downstream of Veazie Dam that were predicted as suitable at all discharges and stages. Also, the reach near the Brewer boat launch was predicted to be suitable for spawning at all discharges and stages.

Table 1.4. Percent weighted usable area (WUA) spawning habitat 1 km below Veazie Dam. Discharge is in cubic meters per second. WUA was determined using combined (depth and velocity) suitability and a modified HSI curve.

Discharge	High	Mid	Low	Average
412	0.35	0.22	0.20	0.26
580	0.23	0.14	0.13	0.17
793	0.18	0.12	0.11	0.14
1009	0.16	0.12	0.11	0.13
1308	0.15	0.14	0.13	0.14

1.4.3 Passage Analysis

Passage suitability declined over the entire Bangor Dam remnants cross section at higher discharges and lower tidal stages (Figure 1.9). Low tidal stage models, at all discharges, had the lowest average passage suitabilities over the entire cross section and in each quarter. Conversely, average passage suitability was greatest for all high tidal stage models at each discharge. While the lowest average passage suitability (0.25) was

predicted for the 1308 cms low stage model, there were still areas within the cross section where passage should be un-inhibited. These passable areas are primarily in the far East quarter of the cross section (Figure 1.10). In this region, depth is greater and water velocities are lower than in the West half of the cross section.

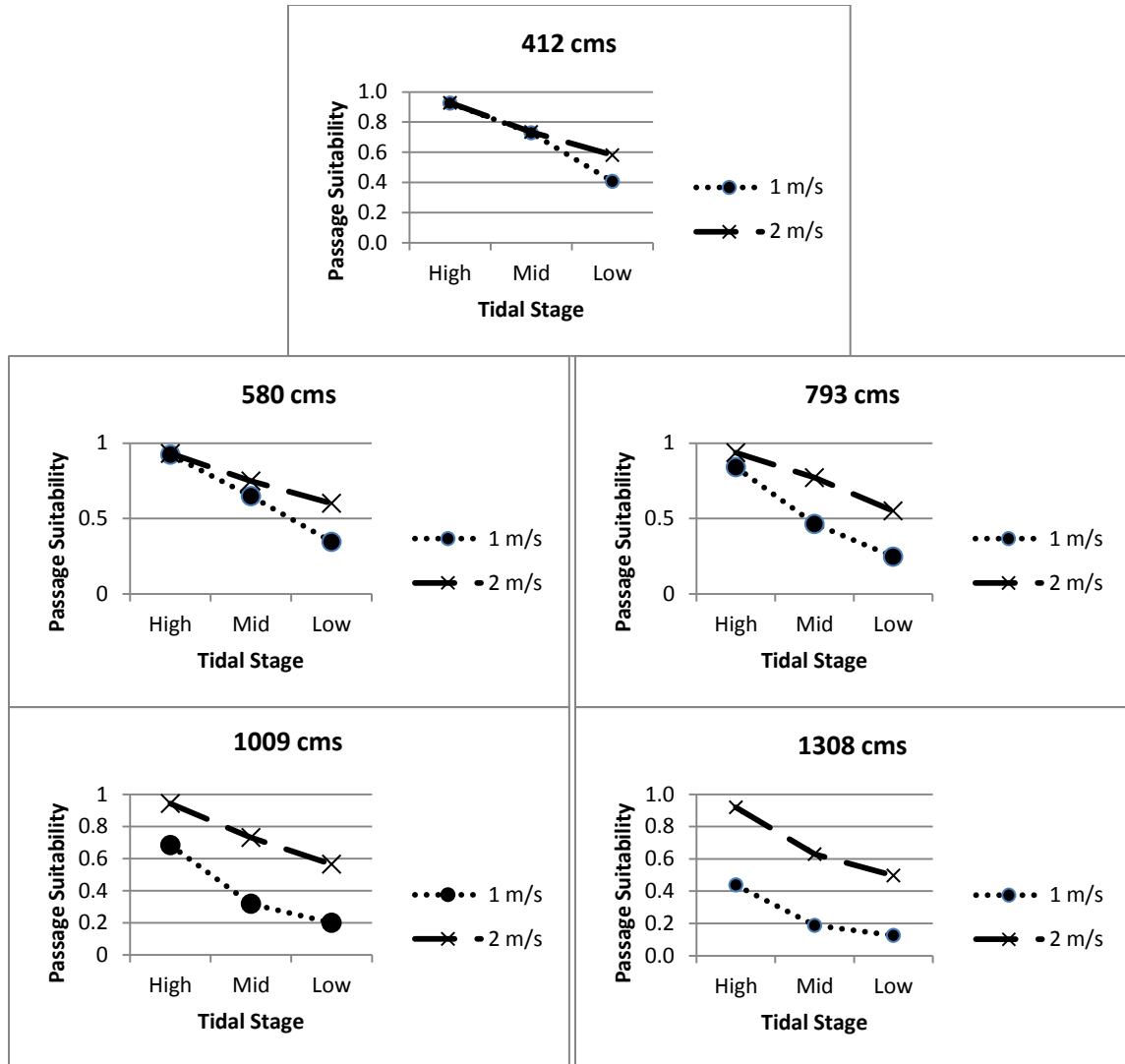


Figure 1.9. Average passage suitability. These graphs contain the average passage suitability of each modeled discharge and tidal stage at the Bangor Dam. The two different swimming performances modeled are noted as 1 m/s and 2 m/s (see Figure 1.7).

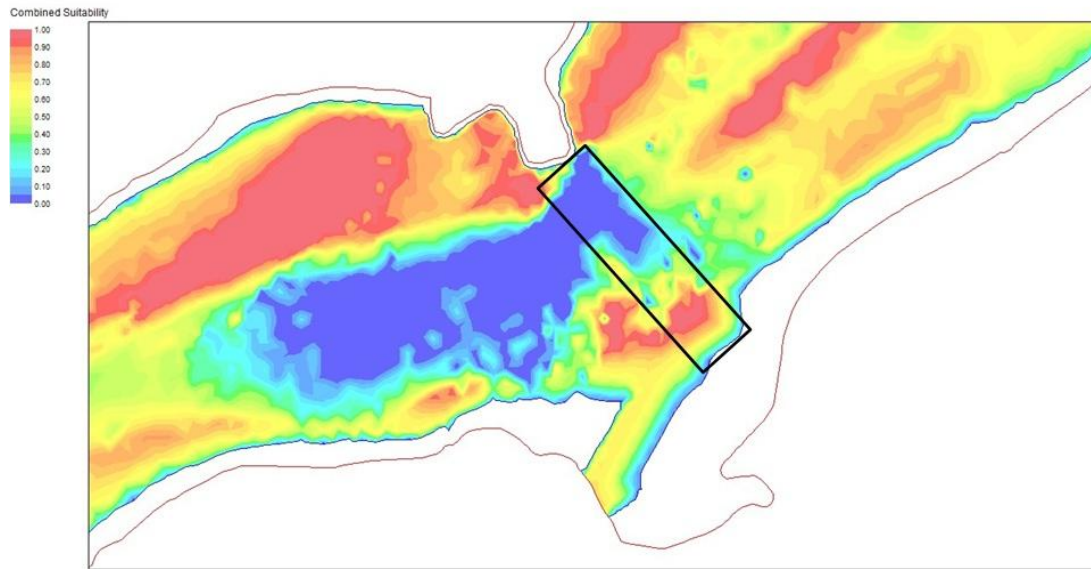


Figure 1.10. Passage suitability of 1009 cms low stage model. The box represents the cross section used for passage suitability analysis. This image shows passage suitability of the 1009 low stage model with the 1m/s swimming performance curve. Warmer colors represent areas of higher passage suitability.

1.5 Discussion

Model results predict suitable spawning habitat within the Penobscot River at all spring discharges and tidal stages modeled. Directly downstream of the Veazie Dam, where spawning is expected to occur, based on observations in other river systems, predicted spawning habitat is restricted to small areas along the margins of the channel. Another area predicted to be suitable is adjacent to the Brewer boat launch. These areas are consistently predicted to be suitable for spawning at all discharges and tidal stages. Additionally, the Bangor Dam passage analysis indicates that shortnose sturgeon should be capable of successful passage and able to reach suitable spawning habitat below the Veazie Dam during several spring discharge conditions.

1.5.1 Spawning Habitat

Although, spawning habitat analysis suggests that there is little suitable habitat directly below Veazie Dam, there are a few areas that are consistently predicted to be marginally suitable immediately downstream of the dam. These areas are located near shore, extending 30 to 40 m from each bank. Most of these areas should be considered marginally suitable because the majority of their suitability indices are 0.6 or less. Within these larger, marginal areas there are smaller areas of highly suitable habitat with indices ranging from 1.0 to 0.7. On the channel side of the smaller areas suitability is likely reduced by increasing water velocities. While on the bank side, decreasing depths are the controlling parameter. Overall, it appears that there are few persistent areas with suitable velocity and depth below the Veazie Dam for spawning.

The bulk of highly suitable spawning habitat estimated by the models is near the channel edge beginning about 3km below Veazie Dam and extending to the downstream boundary of the model. The total area represented by this reach masks trends in spawning suitability in the first kilometer below Veazie Dam. However, when comparing trends between the whole model and the 1 km sub-section, it becomes clear that the same trend is present (see Figure 1.8). Although, this simulation cannot account for the effect of an incoming tide on spawning habitat, it is important to note that water velocity is the dominant parameter determining spawning suitability within this study and in spawning site selection in rivers with a preponderance of boulder and cobble substrate.

While shortnose sturgeon spawn in a wide range of depths (1.2 – 10.4 m), they have only been observed spawning in a narrow range of water velocities (0.4 – 1.8 m/s) (Kynard 1997). Water velocities in the Penobscot River can change significantly over the

course of a tidal cycle and have a large effect on the prediction of likely spawning habitat. However, tidal influence should not affect water velocities during high spring flows as much as low flows outside of the spawning season when flow reverses all the way to Bangor (rkm 39). Modeled water velocity error associated with tidal influence should be the least during the spring runoff and shortnose sturgeon spawning season. More importantly, the probable under-prediction of water velocities in the models must be considered because this could lead to an over-estimate of suitable spawning habitat and alter the spatial distribution of suitable areas. Although, these models cannot accurately predict water velocities throughout the entire tidal cycle, they do provide discrete estimates for certain portions of the cycle. These models are a close approximation of spring river conditions and are useful for predicting the habitats that might serve as the best spawning sites under the modeled conditions.

Highly suitable habitat in the downstream reach adjacent to the Brewer boat launch becomes less likely to host spawning sites when other elements of shortnose sturgeon biology are considered, especially larval biology. Shortnose sturgeon larvae migrate downstream from spawning sites via swim up and drift behavior over a period of two to 14 days (Kynard 1997). While the distance of their downstream migration in the Penobscot River is unknown, they would not have to travel far (7.5 km from the base of Veazie Dam) to be exposed to salt wedge intrusion in the summer months. Townsend (1985) documented salt wedge intrusion commonly extending to the mouth of Kenduskeag Stream during summer months and occasionally to Bangor Dam. The confluence of Kenduskeag Stream is located 7.5 rkm from Veazie Dam and 2.4 rkm from Bangor Dam. Consequently, the position of the salt wedge in the summer could be a

determining factor of spawning site suitability as young of year shortnose sturgeon do not develop salinity tolerance until about one year of age (Ziegeweid et al. 2008).

In the Connecticut River shortnose sturgeon larvae were captured at a maximum distance of 15 km downstream from a known spawning site and were estimated to move 7.5 km per day (Kynard and Horgan 2002). If shortnose sturgeon spawning were to take place below Veazie Dam, a portion of progeny would likely encounter fatal salinity levels before developing salinity tolerance. However, if spawning were occurring immediately downstream of Veazie Dam it is likely that some larvae would cease migration upstream of the summer salt wedge intrusion and survive. Townsend's (1985) data collection occurred between 1963 and 1977, before the Bangor Dam was removed. The effect of the Bangor Dam breach on summer salt wedge intrusion is unknown; however, it is unlikely to significantly alter the extent of summer salt wedge intrusion. Upstream movement of spawning shortnose sturgeon adults is necessary to provide ample freshwater habitat for larval maturation and prevent the exposure of larvae to fatal salinity; requiring adults to pass upstream of the Bangor Dam remnants.

1.5.2 Passage

Model analysis of the Bangor Dam reach indicates that shortnose sturgeon passage should be un-inhibited at the modeled spawning season discharges, which reflect river conditions during five spawning seasons. However, calibration problems arising in the low tidal stage models could affect the results by overestimating passage suitability. In addition, passage estimates could also be overestimated due to probable underestimation of water velocities within high and mid tidal stage models. There are

other factors affecting passage that are either unknown or difficult to model accurately. These factors include swimming capability, tidal fluctuations in velocity, and the influence of bathymetry on behavior. Measures of shortnose sturgeon sustained and burst swimming speeds, which are not available, were estimated from lake sturgeon swimming performance data.

It should be noted that passage was assessed for multiple swimming capabilities. Modeled shortnose sturgeon swimming capability had a large effect on passage suitability estimates (see Figure 1.9). The results from different swimming speed analyses are intuitive. Lower values of maximum passable water velocities produced smaller average suitability and WUA estimates than higher maximum passable velocity values. While the lowest swimming capability, diminishing from un-inhibited passage at 1 m/s to zero passage at 2 m/s, resulted in diminished passage suitability, there were still passable areas. Also, the model with the lowest passage suitability, 1308 cms low tide, retained 13 percent passage by area.

Calibration to measured depth values was restricted for all low tidal stage models, the 1009 cms mid tidal stage model, and all 1308 cms models. The compromise reached in selecting these models resulted in depths at the Bangor Dam remnants being deeper than measured depths corrected to the USGS gauging station. Within River 2D, deeper depths in this area would result in a reduced depth-averaged water velocity. It is likely that actual water velocities at the Bangor Dam remnants are higher than water velocities estimated by the model. These remnants form a shallow feature that extends across the width of the river. The most extreme portion of this feature extends half way across the river and over a distance of approximately 4 m abruptly transitions from a high tide water

depth of 3-4 m upstream of the remnants to 1-1.5 m at the remnant lip. This abrupt change results in a significant hydraulic jump and super critical flow is present between mid and low tides.

Consequently, once the hydraulic jump forms at the Bangor Dam, the accuracy of the River 2D solution breaks down. This problem is not restricted to just River 2D, as hydrodynamic modeling becomes difficult immediately adjacent to hydraulic jumps within extant two dimensional hydrodynamic models. To accurately assess water velocities at the Bangor Dam remnants, empirical observations need to be collected at the remnants during spring discharges. If actual water velocities are higher than estimated velocities then this analysis would be an overestimate of passage suitability.

In addition to swimming performance, other behaviors could be important for passage suitability. Bathymetry at the Bangor Dam remnants is highly complex, featuring a shallow constriction upstream that tails out over a mid-depth plateau. This plateau terminates in an abrupt drop into the 9.0 m deep channel. The channel transitions across the river East to West, below the plateau. During fall 2011, a large number of shortnose sturgeon were captured at the upstream end of the channel on the West side of the river (Altenritter unpublished data). If shortnose sturgeon use the channel to move upstream in the spring, it would place them on the West side of the river. If this is the case, sturgeon would have to move across the highest velocity areas of the reach to gain access to lower velocities on the East side of the river. Shortnose sturgeon implanted with acoustic tags have been tracked during the spring spawning season but none have moved to this section of the river (Chapter 2) as such, shortnose sturgeon movement patterns while passing the Bangor Dam in the fall are unknown.

Passage at the Bangor Dam remains an important question. It is not known if sturgeon pass upstream of the remnants in the spring, though passage in the summer and fall has been documented. An acoustic receiver array has recorded 48 out of a total of 96 shortnose sturgeon with acoustic tags upstream of the remnants in the summer and fall between 2006 and 2011. However, on the dates of likely passage, discharge was well below average spring spawning season discharge. Furthermore, upstream movement from the overwintering site has not been detected during the spring spawning window in four years of monitoring. Model results suggest that shortnose sturgeon can successfully pass the Bangor Dam remnants although passage has not been observed during high spring discharges.

1.5.3 Model Resolution

Crowder and Diplas (2000) demonstrated the importance of accurate bathymetry for hydrodynamic modeling by constructing multiple models of the same reach and gradually including bathymetric data of several large boulders. Not surprisingly, the model with the best representation of the boulders most accurately modeled observed flow features within the reach. Detailed bathymetry collected in the Bangor Dam reach produced a digital elevation model with high resolution (2 m grid). Due to high resolution bathymetry surveys in this reach a much smaller mesh spacing (10 m) was used than in the rest of the modeled domain (20 m). However, bathymetry surveys revealed a highly variable river bottom; a mesh spacing closer to 2 m would be preferable.

Bathymetry surveys conducted upstream and downstream of the Bangor Dam reach were widely spaced (see Figure 1.2) and not capable of producing the same resolution as data collected in the Bangor Dam reach. To create a more accurate model of the entire reach from Veazie Dam to Kenduskeag Stream, additional bathymetry needs to be collected. Bathymetry collection should focus on filling in data gaps and additional surveys in areas with complex bathymetry. Currently, large areas of highly variable bathymetry have not been surveyed, and thus, are not represented in the model. This lack of data has certainly led to a less than satisfactory representation of the river bed in areas of interest, such as immediately downstream of Veazie Dam. Nevertheless, these areas are represented in the models described above and the spawning habitat suitability results should be considered in light of the limited bathymetry in certain areas.

1.6 Conclusions

Model results indicate that there is suitable spawning habitat below the Veazie Dam and adjacent to the Brewer boat launch. However, proximity to the summer salt wedge intrusion could significantly reduce suitable spawning habitat in the lower reaches of the modeled domain. In addition, shortnose sturgeon should be capable of upstream passage across the Bangor Dam remnants. However, empirical surveys conducted at spring discharges are needed to verify passage analysis results. Following the removal of Veazie Dam and Great Works Dam, shortnose sturgeon will have access to an additional 14.8 rkm. Though passage at the Bangor Dam remnants, will need to be addressed to ensure restoration activities to have a positive effect on the shortnose sturgeon population in the Penobscot River.

CHAPTER 2

SHORTNOSE STURGEON REPRODUCTION AND ACOUSTIC TELEMETRY IN THE PENOBSCOT RIVER, MAINE: EVIDENCE OF A GULF OF MAINE METAPOPOPULATION

2.1 Abstract

Shortnose sturgeon (*Acipenser brevirostrum*) of the Penobscot River were monitored with acoustic telemetry. Telemetry results indicate a high rate of exchange between the Penobscot and Kennebec Rivers. Most telemetered females with eggs in the late stage of development that overwintered in the Penobscot left the river system prior to suitable spawning conditions. No upstream movements were detected during presumed favorable spawning conditions in the Penobscot River. Nine hundred twenty-two hours of D-net sampling and 6,648 hours of artificial substrate sampling failed to capture shortnose sturgeon eggs or larvae in the Penobscot River. Also, females with late stage eggs were later detected at known spawning areas in the Kennebec and Androscoggin rivers during suitable spawning conditions. These results indicate that currently the Penobscot is unlikely to host spawning and suggest a metapopulation or patchy population structure within the Gulf of Maine.

2.2 Introduction

The spatial distribution of a species can vary on multiple scales, whether it is across their geographic range or within a habitat patch. Populations, distributed within a geographic range, can be considered within a metapopulation framework if they occur in

patches yet exhibit a certain degree of connectivity, linking local and large scale processes (Hanski and Gilpin 1991, Kritzer and Sale 2004, Girard et al. 2010). Local populations are assumed to be self-sustaining, and their dynamics largely driven by internal trends and local environmental conditions. Understanding metapopulation structure is conditional on knowing if reproduction is occurring within each local population. Additionally, migrants among local populations are not typically thought to play a large role in local population dynamics, yet migrants are a vital component of metapopulation maintenance. Management of metapopulations hinges on assessment of local population dynamics, quantification of connectivity, and identification of dispersal corridors (Kritzer and Sale 2004).

The management of threatened or endangered species, particularly of recently discovered populations, depends on understanding the internal dynamics of the recently discovered population and its interactions with other demes. If individuals are cryptic and populations spread over large geographic areas, it is possible that metapopulation dynamics are occurring, even if not immediately obvious. For example, in 1994 an unknown population of the threatened Black Rail (*Laterallus jamaicensis*) was discovered in the foothills of the Sierra Nevada Mountains (Girard et al. 2010). Genetic evidence revealed a metapopulation structure of multiple self-sustaining populations with low rates of movement among populations. Additional management protections for likely migration corridors were recommended based on their results (Girard et al. 2010). The black rail case highlights the necessity of acquiring accurate local population information and the extent of connectivity. In this example, primary research questions included ways to assess the population's overall size, health, demography, and degree of

connectivity with nearby populations (Girard et al. 2010). For many such populations, once these characteristics are identified, management plans protecting or used to recover endangered and threatened species can be modified to account for newly discovered habitat or dispersal corridors.

Determining the reproductive status of cryptic endangered species, such as a recently discovered sturgeon population in the Gulf of Maine, is critically important to understanding population structure and establishing appropriate management strategies. Shortnose sturgeon (*Acipenser brevirostrum*), an endangered species recently found inhabiting historic habitat following a 28 year gap in observations in the Penobscot River, has similar features to the black rail metapopulation. Prior to 2006, the last documented shortnose sturgeon captured in the Penobscot was in 1978 (Squires and Smith 1979). Since an angler's report of landing a sturgeon in 2005, researchers have captured 454 individual shortnose sturgeon between 2006 and 2009 (Fernandes et al. 2010, Dionne et al. submitted). Dionne (2010) estimated the population within the Penobscot River to be 1,654 (95% CI: 1108 – 2200) in 2009. This population is currently listed as one of 19 distinct population segments under the US Endangered Species Act with recovery measures identified in the *Shortnose Sturgeon Recovery Plan* (National Marine Fisheries Service 1998). However, research in the Penobscot River has documented coastal movements between river systems, suggesting a patchy or metapopulation structure (Fernandes et al. 2010, Dionne et al. submitted). Discerning among such population structures requires, in part, some understanding of whether a deme is supported by varying degrees of internal or external production. Such production has not been documented in the Penobscot.

The extent of movement and habitat use of Penobscot shortnose sturgeon has been investigated using acoustic telemetry (Fernandes et al. 2010, Dionne et al. submitted). Observations of shortnose sturgeon captured in the Penobscot River and surgically implanted with acoustic tags (n=46, 2006 – 2008) revealed extensive use of the marine environment including long distance movements (>150km) between the Penobscot and Kennebec Rivers in the Gulf of Maine (GoM) (Fernandes et al. 2010, Dionne et al. submitted). In addition, two shortnose sturgeon tagged with passive integrated transponders in the Kennebec River in 1998 and 1999 were recaptured in the Penobscot River in 2007 (Fernandes 2008). Of the sturgeon implanted with acoustic tags in the Penobscot River, 72% left the Penobscot estuary into the marine environment for a period during the life of the tag (Dionne et al. submitted). These observations are strong evidence contradicting the most common portrayal of shortnose sturgeon life history, natal river residency throughout their life span (Kynard 1997, Bain 1997).

Shortnose sturgeon in reproductive condition typically spawn in the same river system that they overwinter (Dadswell et al. 1984, Kynard 1997) and hundreds of shortnose sturgeon have been documented wintering in the Penobscot River (Fernandes et al. 2010; Lachapelle unpublished data). In un-impounded river systems, shortnose sturgeon migrate great distances, up to 200km, upstream to spawn in the spring (Kynard 1997). However, in impounded river systems spawning typically takes place in close proximity to the first barrier to upstream movement (Kynard 1997, Duncan et al. 2004). Currently, the lowermost dam on the Penobscot River is located at the head of tide at river kilometer (rkm) 46. Historically, shortnose sturgeon had access to Milford Falls, presently the site of Milford Dam (rkm 62). The natural falls at Milford and Gillman

Falls on the Stillwater River probably limited access to additional habitat. It is likely that if spawning historically occurred in the Penobscot, it occurred below either of these falls.

The current situation is about to change as river restoration activities are underway on the Penobscot River. The Penobscot River Restoration Trust is coordinating the removal of the two lowermost dams, Veazie Dam and Great Works Dam, constructing a fish lift at Milford Dam, and a bypass around Howland Dam (Opperman et al. 2011). These restoration activities will restore sturgeon access to 100 percent of their historic range in the mainstem Penobscot River. However, the Stillwater River will remain dammed and in-accessible to sturgeon. Nevertheless, the response of shortnose sturgeon to Penobscot River dam removals has the potential to significantly alter population dynamics within the Penobscot and the GoM. The restoration of historic spawning habitat could lead to increased recruitment in the Penobscot and alter immigration/emigration patterns between the Penobscot and Kennebec Rivers.

The presence or absence of a reproducing population in the Penobscot River was investigated because of uncertainty associated with the presence of large numbers of wintering sturgeon in the Penobscot, the high degree of connectivity between river systems, and knowledge of spawning in the Kennebec River (Wippelhauser and Squiers submitted). Additionally, acoustic telemetry observations from 2006 to 2009 did not provide evidence of upstream movements in the Penobscot River; typical of shortnose sturgeon spawning behavior during the expected spring spawning window (Dionne unpublished data). Eleven of the 46 sturgeon with acoustic tags migrated to the Kennebec River; of the 11, four were identified as females with late stage eggs (gravid females; Dionne et al. submitted). These fish left the Penobscot River prior to water

temperatures rising into commonly regarded spawning ranges, 9°C - 15°C (Kynard 1997). However, 78% of these fish were detected near known spawning grounds in the Kennebec River when water temperatures were suitable for spawning (Dionne et al. submitted; Wippelhauser unpublished data).

Sampling for eggs or larvae is considered the most direct means to assess local reproduction in sturgeon (Kieffer and Kynard 1996, Brown 1997). However, such sampling has only recently been undertaken in the Penobscot River. In addition, because acoustic telemetry was very successful in documenting different migratory strategies within the Penobscot River population (Dionne et al. submitted), additional efforts were focused on increasing assessment of gravid females and their pre-spawn, spring movements. This work centered around three major questions to better understand the structure of the Penobscot River shortnose sturgeon population and how it relates to populations in the Kennebec and Androscoggin Rivers. Are shortnose sturgeon eggs or larvae present within the Penobscot River? Are spring movements of gravid females most consistent with spawning in the Penobscot or with spawning in the Kennebec-Androscoggin system? Finally, what was the probability of failing to tag a shortnose sturgeon in reproductive condition?

2.3 Methods

2.3.1 Study Area

This study took place between the estuary and lowermost dam on the Penobscot River, Maine. The Penobscot is the largest watershed in the state of Maine that drains into the GoM. Human activities have occurred in this watershed for approximately 9,000

years. However, it was not until the early 1800's that human activities significantly impaired sturgeon habitat in the Penobscot River (Opperman et al. 2011). Timber extraction and processing (e.g., lumber and paper mills), dam construction, urbanization, and dredging resulted in significant water quality and habitat impairment for much of the next century. Currently, water quality has significantly improved under more stringent state and federal regulations (Federal Energy Regulatory Commission 1997). The study area is shown in Figure 2.1.

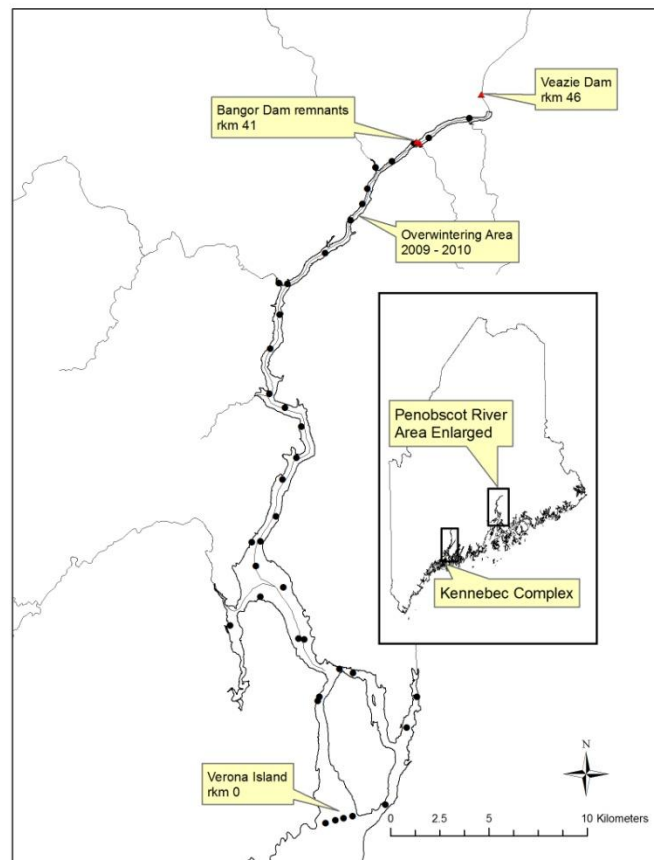


Figure 2.1. Study area. This map shows the reach of the Penobscot River where acoustic telemetry and sampling for spawning activities were conducted from 2009 - 2011. Black points represent acoustic receiver (Vemco, VR2 or VR2W) stations within the Penobscot River acoustic array. The inset indicates the relative location of the Kennebec-Androscoggin system to the Penobscot.

2.3.2 Field Methods

In an attempt to follow mature shortnose sturgeon to spawning habitat, adult shortnose sturgeon were captured between June and October in 2009 ($n = 221$) and 2010 ($n = 197$) with bottom-set, 16.2 cm stretch, multifilament gill nets that were 2.5 m by 90 m and a subset tagged with acoustic transmitters. Once captured, sturgeon were placed in a floating net pen prior to processing. Standard processing consisted of the following. Fish were scanned for a passive integrated transponder (PIT) tag, if not detected a PIT tag was injected into the muscle anterior and ventral to the dorsal fin. Additionally, fish were given unique, numbered floy tags, if an external tag was not present. Total length (cm), fork length (cm), weight (kg), inter-orbital distance (mm), and inner and outer lip measurements (mm) were taken from each fish. A picture was taken of the dorsal and ventral surfaces of each fish along with an identifying number. Finally, the reproductive condition of all fish was examined via borescope using the methods of Kynard and Kieffer (2002). Reproductive condition could only be determined for females with developing eggs. Fish chosen for acoustic tag implantation were then held in a floating net pen in preparation for surgery and all others were released following processing.

Fish chosen for surgery were placed in a cloth sling suspended in a trough of river water. Prior to surgery, fish were anesthetized by adding a buffered solution of MS-222 (tricaine methane sulfonate) to the water. Surgery did not proceed until fish were minimally responsive. Acoustic tags were inserted into the body cavity through a 3 cm incision on their ventral surface approximately 10 cm behind the pectoral fins. Tags were inserted forward and the incision sutured: a first set of sutures were passed completely through the epidermis and underlying fatty tissue with absorbable 3-0 chromic gut; a

second set of sutures (3-0 silk) were passed through the epidermis, but not into the body cavity. Following surgery, fish were placed into the floating net pen and allowed to fully recover from anesthesia before release.

Tags implanted were individually coded Vemco V-13-1L acoustic tags that weighed 12g in air and measured 13 mm by 36 mm. All tags (n=53) transmitted at 69 kHz. All but 18 tags transmitted at 90 (± 15) s intervals for the entire life of the tag. The remaining 18, implanted in October 2010, were programmed with ping rates that changed by season to facilitate more detailed active tracking during some seasonal windows (late fall and spring). When first activated these tags transmitted at 30 s intervals for 60 d, did not transmit for 140 d, transmitted at 30 s intervals for 40 d, and then transmitted at 90 s intervals for the remainder of tag life. These 18 tags were activated on September 7, 2010 and had an expected tag life of 1,005 days. The remaining tags were implanted between August 3, 2009 and September 10, 2010.

2.3.3 Acoustic Telemetry

An acoustic receiver array was deployed in the Penobscot River consisting of Vemco VR2 and VR2W receivers at thirty four receiver stations from the southern end of Verona Island (rkm 0) to the base of Veazie Dam (rkm 46; see Figure 2.1). Receivers were deployed in 2010 from March 11 to November 29 and in 2011 from March 16 and November 27. While deployed, receivers were downloaded approximately every other month. Also, two receivers were deployed up and downstream of the shortnose sturgeon overwintering site in the Penobscot River in the winters of 2007 - 2011. Telemetry data collected in 2010 and 2011 was appended to acoustic telemetry data collected by

Fernandes (2008) and Dionne (2010) from 2006 - 2009. The combined dataset includes data from 2006 – 2011. In addition to the receivers in the Penobscot River, receivers were also deployed in four rivers between the Penobscot and Kennebec Rivers from 2008 - 2011. Receivers (n=8) were located in the Passagassawakeag River (1), St. George River (2), Medomak River (2), and Damariscotta River (3). Finally, the Maine Department of Marine Resources maintained an acoustic receiver array of 14 receivers in the Kennebec and Androscoggin Rivers from 2007 - 2011.

Range testing was conducted to investigate the possibility of a tagged fish moving upstream from the overwintering site undetected. Range testing was conducted in the spring of 2011 at a discharge of 1,580 cms at the first VR2 receiver upstream of the overwintering site. An active Vemco V-13 tag was attached to a rope 0.3 m above a 2.0 kg weight that was lowered at various locations to a depth of 2.5 m below the boat. When activated, this tag transmitted a quick series of 10 closely spaced pings that we attempted to detect with a VR-100 omni-directional receiver that logged the tag detection time, tag code, and UTM location. The VR-100 was located on the boat and the hydrophone suspended adjacent to the acoustic tag. A total of ten drifts beginning directly adjacent to the VR2 receiver and moving away were conducted. Following the last drift, the VR2 receiver and VR-100 were downloaded. Successful detections at the receiver were then correlated with tag position by coupling VR2 receiver data and VR-100 detection and GPS data.

The likelihood of detecting a gravid female sturgeon moving upstream to potential spawning habitat is expected to be dependent in part on the probability of tagging overwintering fish in reproductive condition. Hence, the probability of failing to

tag a reproductively mature shortnose sturgeon that overwintered in the Penobscot River during the winters of 2006 – 2010 was estimated. Preliminary overwintering population estimates (Lachapelle unpublished data) were used to determine the number of individuals likely to spawn the following spring based on spawning intervals of three to five years for females and one to three years for males (Dadswell et al. 1984). These intervals were used to generate best and worst case estimates. The number of active tags in the system each spring was accounted for by filtering tags out of the analysis that were expected to stop operating and those that were stationary for more than two months during the spring, summer, or fall (potential expelled tags or mortalities, as in Dionne et al. submitted). The total number of unique individuals that overwintered in the Penobscot during the winters of 2006 – 2010 was 57.

In the winter of 2010, the preliminary overwintering population estimate was 672 (95% CI: 225-1870; Lachapelle unpublished data). The 2010 population estimate was used for all analyses. Assuming that fall emigration is random with respect to maturation condition and an equal sex distribution, 336 of these fish would be male and 336 would be female. The probability that none of our fish tagged with acoustic transmitters included these potentially maturing individuals was then calculated for each combination of male and female spawning periodicity. These probabilities ignore the known gravid females implanted with acoustic tags in each year. Furthermore, a scenario involving a small subset of the overwintering population being local, Penobscot River spawners was also investigated. In this instance a percentage of overwintering fish were assumed to spawn locally in the Penobscot with the same periodicity. The percentages assessed were 20%, 10%, and 5%. In each case the probability of failing to tag a reproductive, local

spawner was calculated for each year (2006 – 2010). The probabilities from each year were then multiplied to determine the likelihood of failing to tag a Penobscot spawner over the course of the study.

2.3.4 Spawning Sampling

Spawning sampling began in spring 2008 – 2011 when fish were detected moving out of the overwintering area, or as water temperatures increased to 5°C. Sampling ceased on June 30 or when water temperatures reached 25°C, whichever came first. Sampling gear consisted of artificial substrates and modified ichthyoplankton nets (D-nets) to target shortnose sturgeon eggs and larvae, respectively. Both artificial substrates and D-nets have been used successfully to collect sturgeon eggs and larvae in other river systems (Brown 2007, Kieffer and Kynard 1996, Marchant and Shutters 1996). Sampling locations (Figure 2.2) were chosen based on river conditions, telemetry, and hydrodynamic model predictions (Chapter 1).

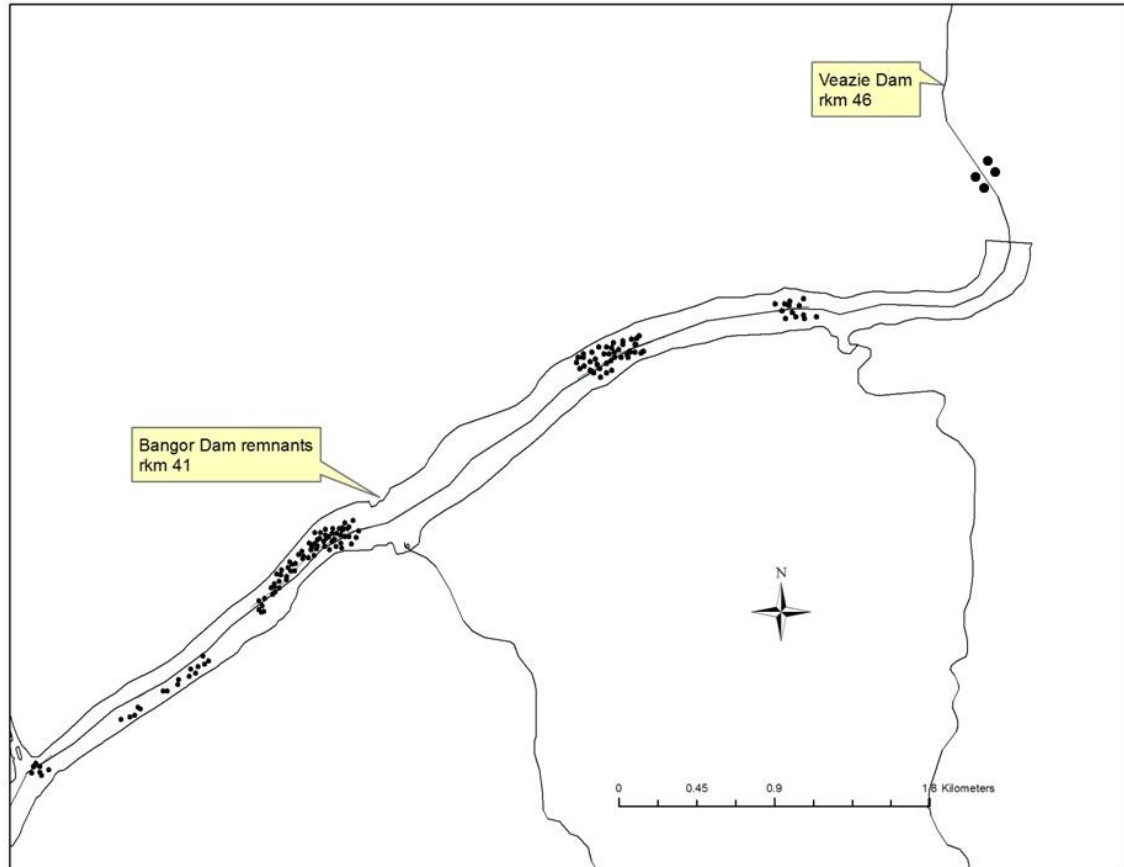


Figure 2.2. Spawning sampling locations: 2010 and 2011. Spawning sampling took place in 2010 between April 8 and June 27 and in 2011 between April 27 and June 24 in the Penobscot River, ME at the points indicated.

Artificial substrate strings consisted of six circular 3M buffer pads (0.71m diameter) attached to 10 m of line with the two end pads strapped to 0.3 m concrete disks. In addition, there was 10 m of line running from the upstream concrete disk to an anchor and buoy lines attached to each concrete disk. D-nets were constructed of 1,000 micron Nytex mesh, were 5 m long and tapered from a 1.0 m x 0.3 m steel frame mouth to a removable 11.4 cm x 30.4 cm PVC collection tube. The D-net was attached via three 1.5 m lines to a single concrete disk that sat on the bottom and was itself attached to a 10 m anchor line. A 10 m buoy line was attached to the top of the D-net frame to maintain the

net mouth in an upright position along the river bottom. To allow retrieval of D-nets during high flows an additional, single, buoy was attached by a 3 m floating line to the main buoys. Sampling location, time deployed, time pulled, and objects collected were recorded for each deployment of artificial substrates and D-nets.

Artificial substrates were set for 48 to 72 h and visually searched for eggs at the end of the set period. D-nets were fished primarily during the ebb tide for two consecutive 3 h sets, at the end of each three hour set they were pulled and collection tube contents emptied into buckets. Collection tube contents were thoroughly searched on the boat between sets. In 2011, D-nets were fished at night from June 16 – 24 (n=6, 213 h) at water temperatures of 18°C - 22°C. To enable safe navigation and retrieval of gear, 12.5 cm glow sticks were attached to each buoy.

2.4. Results

2.4.1 Acoustic Telemetry

Since the inception of shortnose sturgeon research in the Penobscot River in 2006 a total of 96 adult shortnose were implanted with acoustic tags. A total of 38 shortnose sturgeon were implanted with acoustic tags in 2009 (n=11) and 2010 (n=29). During the time frame of this study (2010-2011) there were 27 tags active during the 2010 spawning season and 40 active tags during the 2011 spawning season. However, not all fish with active acoustic tags overwintered in the Penobscot River. Of the 96 individuals carrying acoustic tags 57 overwintered in the Penobscot at least one winter. Telemetry data indicates that there were 11, 11, 10, 14, and 27 fish carrying properly functioning tags that overwintered in the Penobscot in the winters of 2006, 2007, 2008, 2009, and 2010,

respectively. In 2009 there was one confirmed gravid female of the 14 fish with active tags. In 2010, there were four confirmed gravid females of the 27 fish with active acoustic tags. Also, between 2006 and 2008 there were an additional three confirmed gravid females that overwintered in the Penobscot River.

The acoustic receiver array was deployed and recording data prior to shortnose sturgeon movement out of the overwintering site in 2010 and 2011. In spring 2010, movement from the overwintering site began on March 19 and continued through April 4. All detected movements were downstream with no evidence of upstream movement from the wintering site. The spring of 2011 was similar; movement from the overwintering site began on April 9 and lasted until April 25. Again, no upstream movement was detected and all fish quickly moved downstream from the overwintering site over a period of 15 d (2010) and 17 d (2011) (Figure 2.3). The timing of movement corresponded with the first major peak in the hydrograph in both 2010 and 2011 (Figure 2.4). Additionally, at the time of downstream movement water temperatures were below the documented range of temperatures for spawning shortnose sturgeon in other systems. Fish departing the wintering site moved downstream to inhabit the lower estuary. This movement of roughly 15 km was made by each individual, on average, in less than one day.

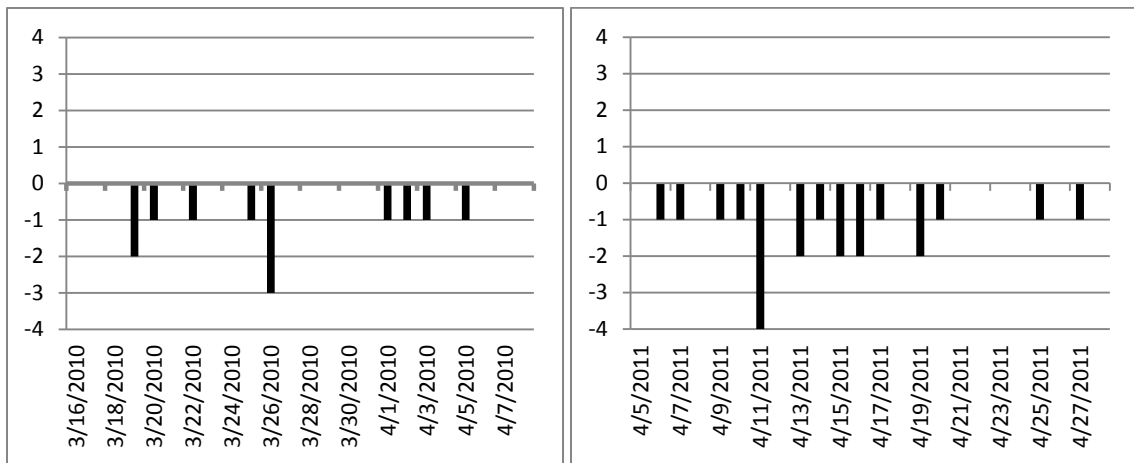


Figure 2.3. Dates of detections up and downstream of the overwintering site: 2010 (left) and 2011 (right). These graphs show the number of fish on a given date detected at the second receiver downstream (negative values) and the first receiver upstream (positive values) of the overwintering site in the spring. All shortnose sturgeon with active acoustic tags in the overwintering area are accounted for in the figure.

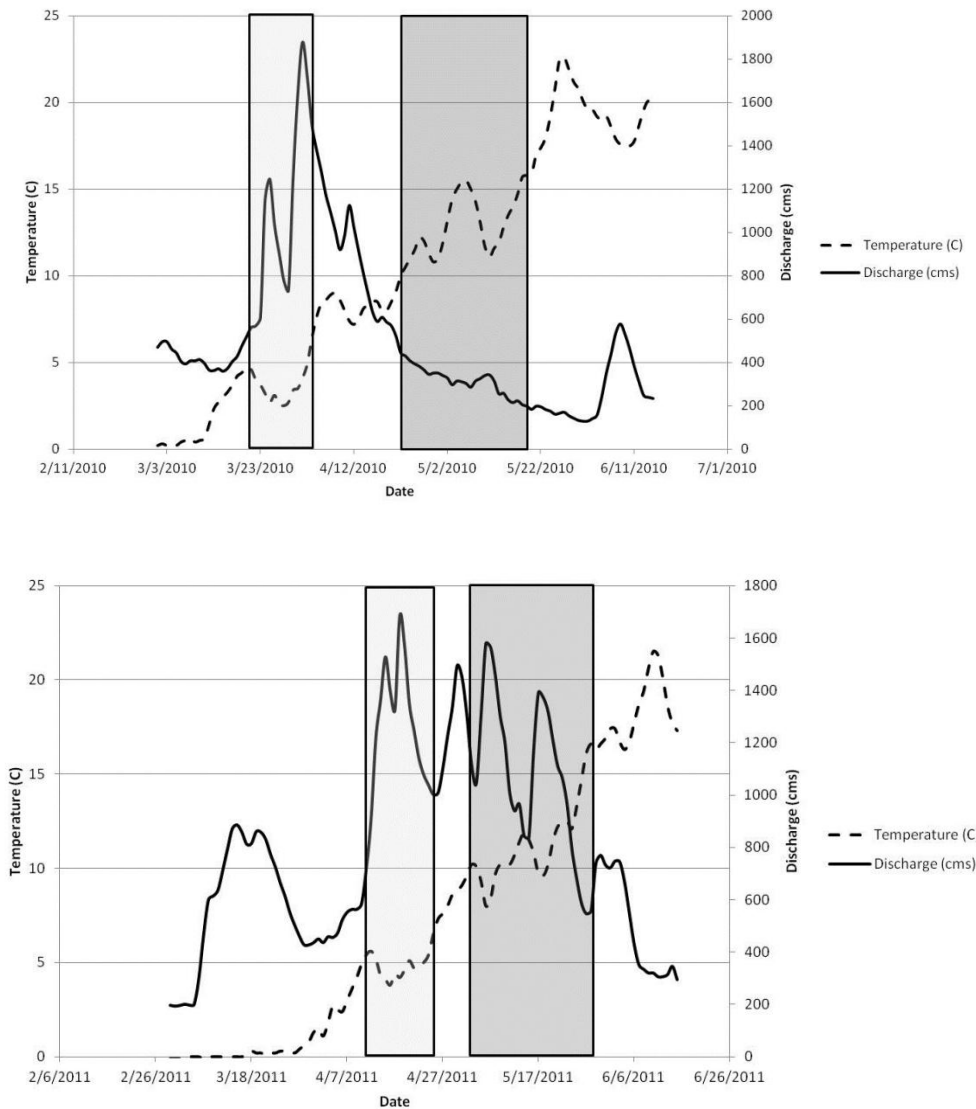


Figure 2.4. Water temperature and discharge in the Penobscot River in spring 2010 (top panel) and 2011 (bottom panel). These graphs show water temperature and discharge data obtained from USGS gauging stations on the Penobscot River. The unshaded box on both panels depicts the time period during which all shortnose sturgeon with acoustic tags moved downstream from the overwintering site in the spring. The shaded box depicts the time period when conditions, discharge and water temperature, in the Penobscot River were presumed favorable for spawning (based on Kynard 1997).

Shortnose sturgeon that remained in the Penobscot, stayed in the lower estuary until discharge and water temperature were well out of the presumed suitable spawning range of 9°C - 15°C (Kynard 1997). Fish that emigrated to the Kennebec River in the spring made movements that initially mirrored those of resident fish, moving downstream, spending 5 - 19 d in the lower estuary (Fernandes et al. 2010; Dionne et al. submitted), before leaving the Penobscot River altogether. Four shortnose sturgeon, that overwintered in the Penobscot, were detected leaving the Penobscot River in spring 2010 (n=1) and 2011 (n=3) and were subsequently detected in the Kennebec system (complex of the Kennebec, Androscoggin, and Sheepscot Rivers). All shortnose sturgeon that emigrated to the Kennebec system in the springs of 2010 and 2011 were identified as gravid females the previous fall. The time between the last detection in the Penobscot River and first detection in the Kennebec system ranged from 9 to 15 days. The single gravid female that left the Penobscot River in 2010 was detected at a known spawning site in the Kennebec River. Also, two of the three gravid female emigrants in 2011 were detected at known spawning areas in the Kennebec and the Androscoggin Rivers. The remaining female was detected in the Sheepscot River (where spawning has not been documented). Dionne et al. (submitted) documented 10 fish migrating to the Kennebec system in the springs of 2008 and 2009; three gravid females and seven fish of undetermined reproductive status.

Gravid females that emigrated to the Kennebec system did not remain at the spawning areas for long. The sturgeons detected near a spawning area in the Kennebec River remained in the area from April 30 - May 8, 2010 and May 16 - 21, 2011. The sturgeon detected in the Androscoggin River in 2011 was detected at a spawning area

from May 7 - 9. Water temperature data in the Kennebec was only available for spring 2010, and indicated that the female was present at the known spawning area when temperatures rose from 9°C to 15°C (Wippelhauser unpublished data). Following detections at these spawning areas, emigrant shortnose sturgeon then moved back to the Penobscot River. The shortnose sturgeon last detected at a Kennebec River spawning area on May 21 returned to the Penobscot estuary on June 16 after being detected in the Damariscotta River June 6 - 16. The sturgeon last detected at a spawning area in the Androscoggin River on May 9 returned to the Penobscot on May 29 and was not detected in coastal rivers between the Kennebec system and Penobscot River.

Accounting for the remaining spring migrants (n=2) of 2010 and 2011, a female with eggs in the early stage of development, tagged in the fall of 2009, was detected leaving the Penobscot River in the spring of 2010. This fish was subsequently detected in the Kennebec system and remained there until May 27, 2011. This sturgeon would likely have been in reproductive condition in the spring of 2011, when it was in the Kennebec system. However, this fish was not recaptured during this time period and its reproductive condition in the spring of 2011 cannot be confirmed. Additionally, one fish of unidentified reproductive condition was detected leaving the Penobscot River on May 24, 2011, but was not detected in the Kennebec system prior to returning to the Penobscot on July 10. It is not known where this fish was during its time at large. Shortnose sturgeon implanted with acoustic tags that were identified as gravid females and migrated to the Kennebec system the following spring did not migrate to the Kennebec system in successive study years.

In the fall of 2006 – 2010 (with the exception of fall 2009) shortnose sturgeon were detected at the first receiver downstream of Veazie Dam. This receiver is located 2 km downstream of Veazie Dam and 8.5 km upstream of the overwintering site. In both fall 2006 and 2007 three fish were detected, in 2008 and 2010 one fish was detected, and none were detected in fall 2009. These fish were detected in late September through late October as water temperatures decreased. Following their detections at the receiver, they moved downstream and overwintered in the main aggregation. Of these eight fish, one was a confirmed gravid female with mature eggs that were observed during tag implantation surgery seven days prior to the individual's detection at the upstream receiver. An additional gravid female was detected at a receiver 6.4 km upstream of the overwintering site in fall 2009.

2.4.2 Range Testing

Acoustic tag transmissions were detected by the tested VR2 receiver across the width of the river channel (155 m), even though range testing was partially confounded by the presence of acoustic tags implanted in out-migrating Atlantic salmon (*Salmo salar*) smolts. Double crested cormorants (*Phalacrocorax auritus*), a predator of salmon smolts, perched near the receiver selected for range testing, consequently, a handful of these acoustic tags were expelled within range of the selected receiver and interfered with detection of the test tag. Although expelled smolt tags prevented the detection of some test tag transmissions within the series of 10 pings, a sufficient number of pings (>2) were detected by the receiver to conclude that the test tag was within the receivers detection range (Figure 2.5). This interference occurred at all ranges tested.

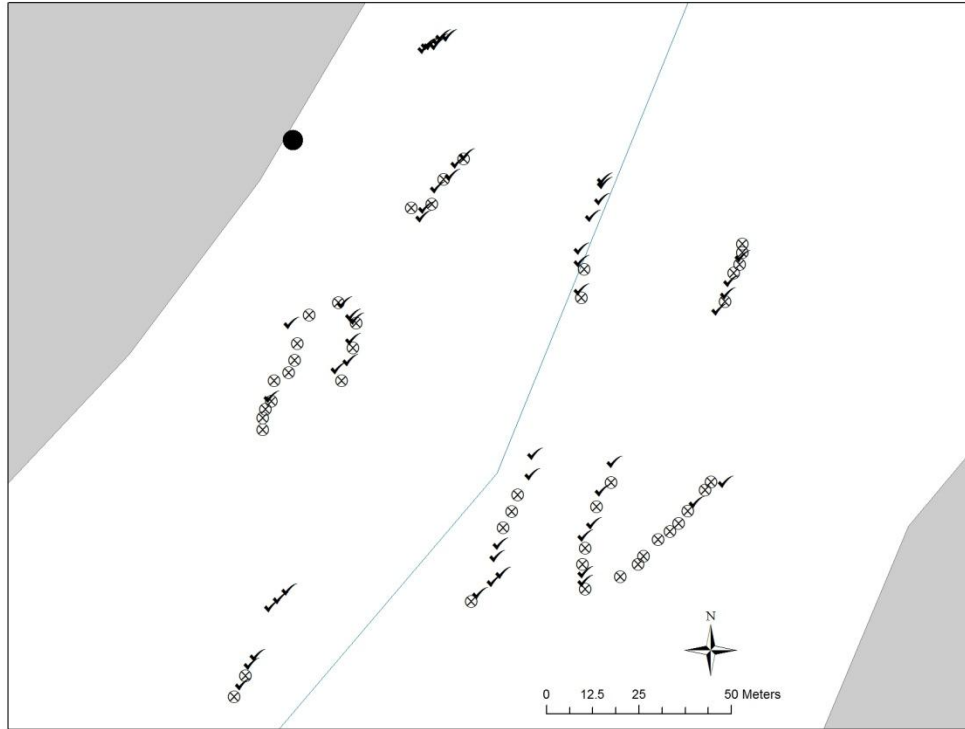


Figure 2.5. Range testing results. This map shows the location of the tested acoustic receiver (large circle), and locations of both successful (check marks), and un-successful (circled X) detections of test tag transmissions.

2.4.3 Tagging Probability

Independent of our knowledge of gravid females, the probability of not having an acoustically tagged fish in reproductive condition overwinter in the Penobscot River was calculated to be as low as 2.5% in 2009 and $<0.1\%$ in 2010 for the worst case scenario of males spawning every three years and females every five years (Table 2.1). In addition, the probability of failing to tag an overwintering fish in reproductive condition between 2006 and 2010 is estimated at $<0.1\%$. These results are based on the proportion of the population expected to be in reproductive condition each year and the number of active tags in the overwintering area.

Table 2.1. Probability of tagging all non-reproductive sturgeon: 2009-2010. This table shows the probabilities of tagging all non-reproductive sturgeon in 2009 and 2010 based on the number of active tags in the overwintering area and a range of spawning periodicities based on Kynard (1997).

		Year	Male Periodicity (years)		
			1	2	3
Female Periodicity (years)	3	2009	<0.001	0.0016	0.0081
		2010	<0.001	<0.001	<0.001
	4	2009	<0.001	0.0036	0.016
		2010	<0.001	<0.001	<0.001
	5	2009	<0.001	0.0057	0.025
		2010	<0.001	<0.001	<0.001

Under the scenario with a subset of the overwintering population comprised of local Penobscot River spawners, the probability of failing to tag a mature individual is higher. For the worst case spawning periodicity and a 20 percent local spawning population subset, the probability of failing to tag one of these sturgeon was predicted to be 1.8%. However, if the local spawning population is reduced to five percent of the overwintering population, this probability increases to 37.1% (Table 2.2).

Table 2.2. Probability of tagging presumed local spawning sturgeon. This table shows the probability of failing to tag at least one locally spawning sturgeon out of a 20%, 10%, and 5% subset of the overwintering population between 2006 and 2010.

		Male Periodicity (years)			
		% Local Spawners	1	2	3
Female Periodicity (years)	3	20	<0.001	0.0018	0.0067
		10	0.0061	0.043	0.082
		5	0.082	0.21	0.29
	4	20	<0.001	0.0034	0.013
		10	0.0085	0.059	0.11
		5	0.096	0.25	0.34
	5	20	<0.001	0.0051	0.019
		10	0.01	0.072	0.14
		5	0.11	0.27	0.37

2.4.4 Spawning Sampling

Spawning sampling took place in 2010 between April 8 and June 27, and in 2011 between April 27 and June 24. D-nets were fished for a total of 922 net hours; 394 h in 2010 and 528 h in 2011. Artificial substrates were fished for a total of 6,648 hours; 2,712 h in 2010 and 3,936 h in 2011. In both years, sampling effort was divided between two river reaches: the Bangor Dam reach and the Brewer boat launch reach (see Figure 2.2). Shortnose sturgeon eggs and larvae were not collected in 2010 or 2011 with either artificial substrates or D-nets. Spawning sampling conducted in 2008 and 2009 failed to capture shortnose sturgeon eggs or larvae (Dionne unpublished data).

While shortnose sturgeon eggs and larvae were not collected, D-nets and artificial substrates captured the eggs and larvae of other species (Table 2.3). Numerous rainbow smelt (*Osmerus mordax*) eggs were found adhered to buffer pads on artificial substrate strings and in the detritus collected in D-Net samples. Additionally, more than 10,000

river herring (*Alosa spp.*) eggs were collected in D-net samples between the years of 2010 and 2011. The majority of captured larvae (n=171) were caught during night D-net sampling. Night sampling occurred in 2011 and accounted for 23.1% of combined 2010 and 2011 D-net sampling effort. However, night sampling accounted for 78.9% of larval captures and 95.2% of river herring egg captures.

Table 2.3. D-Net capture table. This table shows total D-Net captures during the course of spawning sampling in 2010 and 2011. Shortnose sturgeon is abbreviated as SNS in the table.

		SNS Larvae	SNS Eggs	Herring Eggs	Non-SNS Larvae
Year	2010	0	0	418	11
	2011	0	0	>10,000	161

Additional 2010 captures: 2 smallmouth bass, 1 American eel elver

Additional 2011 captures: 12 Atlantic lamprey ammocoetes, 5 American eel elvers, 1 red breast sunfish

2.5 Discussion

The shortnose sturgeon population within the Penobscot River either remained undetected between 1978 and 2006, or represents a recent re-colonization by individuals from the Kennebec system. Migration of gravid females from the Penobscot River to the Kennebec system appears consistent with spawning in the Kennebec. Throughout the course of this study, upstream movements indicative of spawning were not observed in the Penobscot. Coupled with the lack of documented shortnose sturgeon eggs and larvae and the low probability of failing to tag a sturgeon in reproductive condition in the Penobscot, the probability of reproduction occurring in this system is very low.

However, while spawning, and related movements were not documented, the possibility of reproduction occurring in the Penobscot River cannot be discounted.

Fernandes (2008), Dionne (2010), and Lachapelle (unpublished data) have all investigated the population size of shortnose sturgeon within the Penobscot River; with different methods and at different times throughout the year. During the summer months Dionne (2010) estimated a population size of 1,654 (95% CI: 1,108-2,200), while Lachapelle's (unpublished data) preliminary estimate of the overwintering population was 672 (95%CI: 225-1,870). Additionally, Fernandes (2008) and Dionne (2010) discovered connectivity with the Kennebec system and also assessed the degree of exchange between systems of shortnose sturgeon implanted with acoustic tags, 72% were detected migrating to the Kennebec system (Dionne et al. submitted). It is now assumed that the shortnose sturgeon populations in the Penobscot River and Kennebec complex have either an open or metapopulation structure.

The presence of successful reproduction in local populations, although not required, is an important component of metapopulation structure. Research from 2008 to present has not yet documented spawning in the Penobscot River. Field methods were selected based on successful sturgeon spawning documentation in other river systems (Kieffer and Kynard 1996, Brown 2007, Duncan et al. 2004). The absence of upstream movement in the spring made the use of acoustic telemetry to target sampling locations impossible. Instead, sampling locations were selected based on hydrodynamic models (Chapter 1). The selected sampling gear was appropriate for the capture of eggs and larvae of shortnose sturgeon as both types of gear successfully captured the eggs and larvae of other species that were of comparable size, within the Penobscot River. Also,

these gear types have been used to confirm eggs and larvae of shortnose sturgeon in the Kennebec system (Wippelhauser unpublished data). However, the possibility that spawning, even if limited, currently occurs in the Penobscot River cannot be absolutely discounted.

Sampling strategies chosen did have limitations due to the relatively small portion of water sampled by D-nets and the limited effectiveness of artificial substrates (Duncan et al. 2004). Likewise, we could not account for all of the potentially mature fish in the system, and if local spawners are a relatively small portion of maturing fish that overwinter, we would have a high probability, 37%, of failing to tag one of those fish in a given year due to the relatively modest number of individuals implanted with tags each year. However, five years of acoustic tagging has reduced the probability of failing to tag a local spawner significantly (see Table 2.3). Additional years of research should greatly improve the odds, if a small number of local spawners are present in the Penobscot. However, over the course of sturgeon research in the Penobscot, the probability that a local spawner, was tagged is 63%, for the worst case scenario.

Although spawning was not documented in the Penobscot River, a combined six years of acoustic telemetry data (two from this project and four from prior work) provide significant insight into the dynamics of the GoM population as a whole and local dynamics in the Penobscot River. Shortnose sturgeon implanted with acoustic tags in the Penobscot River have yet to exhibit movement patterns indicative of spawning within the Penobscot. In other parts of their range, shortnose sturgeon typically exhibit one of two spawning migration strategies within their home rivers, a long one step, or a shorter two-step movement (Kynard 1997). Observed migrations of gravid females tagged in the

Penobscot River may be analogous to these migration strategies. Gravid females leaving the Penobscot River in the spring appear to make a single long migration to the Kennebec system spawning grounds, whereas gravid females migrating to the Kennebec system in the fall make a two step migration, moving initially to overwintering sites in that system, before making a shorter, final migration upstream to spawning sites in the spring (Dionne et al. submitted).

Within the Penobscot River, shortnose sturgeon began moving out of the overwintering site with the first peak in discharge associated with spring snowmelt in both 2010 and 2011, which is consistent with observations from 2007 – 2009 (Dionne et al. submitted). During this peak in discharge, water temperatures remained well below suitable temperatures for spawning (9°C - 15°C; Kynard 1997). While not all sturgeon with acoustic tags moved out of the wintering site at the same time, all moved to the lower estuary within two days of initiating movement. During this time, upstream movement from the wintering site was not detected. We are confident, given our range testing results, that sturgeon with acoustic tags would have been detected if they had moved upstream from the overwintering site.

Gravid females and individuals of unknown sex have been detected making brief upstream movements in the Penobscot River in the fall of each year. The reasons for these movements remain unclear. It is possible that these fish are attempting to find suitable spawning habitat for the coming spring, or they are attempting to find an adequate overwintering site close to spawning habitat. In each instance, the individual returned downstream and overwintered within the overwintering site at rkm 35. Individuals observed making upstream movements in the fall were not detected moving

upstream the following spring. It is conceivable that these fall movements could be related to spawning the following spring, as two of the fish were identified as gravid females. However, both of the gravid females making this fall movement were detected migrating to the Kennebec system the following spring.

Although telemetry observations do not support the hypothesis of spawning occurring in the Penobscot River, they do provide evidence of sturgeon, tagged in the Penobscot, migrating to and from spawning areas in the Kennebec system. As with prior studies, movements between the Penobscot River and Kennebec system were detected during spring, summer, and fall. Of particular interest to this study were individuals undertaking spring migrations. Gravid females ($n=7$) between 2008 and 2011 were detected emigrating to the Kennebec system in the spring, with the exception of one individual which did not leave the Penobscot estuary and also did not move upstream in the spring. Furthermore, these females were detected near known spawning grounds in the Kennebec system while conditions were suitable for spawning (Dionne 2010; Wippelhauser unpublished data). Previously, Dionne (2010) documented three gravid females emigrating to the Kennebec system that were subsequently detected near known spawning areas within the Kennebec system. Also, in spring 2011 three of four gravid females with functional acoustic tags were detected making spring movements from the Penobscot River to spawning areas in the Kennebec system. Observations in 2010 and 2011 were consistent with previous findings that gravid females in the Penobscot River were 19.6 times more likely to migrate to the Kennebec system (Dionne et al. submitted).

Mitochondrial DNA analysis by Wirgin et al. (2010) did not provide evidence that the Penobscot and Kennebec system shortnose sturgeon populations are genetically distinct. It is important to note that their study provides strong evidence of mixing between populations, but cannot specify the river system where spawning is occurring and cannot really distinguish between cases of historic mixing (e.g., recolonization) versus contemporary mixing. Nonetheless their genetic work, along with observations of migrating gravid females from the Penobscot to the Kennebec system, suggests that there is free exchange of reproductive adults between populations, with spawning occurring in the Kennebec system (Wirgin et al. 2010, Dionne 2010). It should also be noted that all genetic samples from the Penobscot River were collected from mature adults. Interestingly, all shortnose sturgeon captured to date in the Penobscot River are considered mature adults, greater than 55 cm fork length (Dadswell et al. 1984, Fernandes 2008, Dionne 2010). By contrast, eggs, larvae and older juvenile stages have been documented in the Kennebec system. Spring migrations from the Kennebec system to the Penobscot River could be occurring, however, there has not been a concerted effort to implant gravid females with acoustic tags within the Kennebec system. To better understand dynamics between populations the next step is to intensify acoustic telemetry research within the Kennebec system.

Between 2006 and 2009, 72% of shortnose sturgeon implanted with acoustic tags were detected leaving the Penobscot estuary and were later detected in the Kennebec system (Dionne et al. submitted). This connectivity calls into question the current National Marine Fisheries Service shortnose sturgeon management plan in the GoM, which stipulates that both the Kennebec system and the Penobscot River be managed as

distinct population segments (National Marine Fisheries Service 1998). The Kennebec – Penobscot shortnose sturgeon populations may not meet the narrow definition of Levin's classical metapopulation, due to high rates of movement between systems and the lack of documented reproduction in the Penobscot River. However, they could be considered a metapopulation based on spatial segregation and connectivity between systems. Kritzer and Sale (2004) argue that the spatial structure of discrete populations and the connectivity between populations should be defining characteristics of metapopulations in the marine environment.

While the Penobscot River and the Kennebec system are separated by over 150 km of marine habitat, they are linked through the exchange of mature adults. Both systems contain shortnose sturgeon summer foraging and overwintering habitat. In addition, suitable spawning habitat is present and spawning has been documented in the Kennebec system, but while suitable, although limited, spawning habitat appears to be present in the Penobscot (Chapter 1), spawning has not been documented. If the Penobscot River lacks adequate spawning habitat, the linkage between systems is extremely important as it provides an avenue for gravid females in the Penobscot River to successfully spawn. Smaller coastal rivers in between the Penobscot River and Kennebec system may also play an important role in maintaining connectivity between the systems by acting as stepping stones. Many shortnose sturgeon migrating between the Penobscot River and Kennebec system utilize these rivers for short durations (Zydlewski et al. 2011).

Regional shortnose sturgeon dynamics within the GoM have the potential to significantly change following river restoration activities in the Penobscot River. Restored access to historic spawning habitat could lead to increased recruitment in the Penobscot River. Increased recruitment could, in turn, have an either positive or negative effect on the number of spring migrants between the Penobscot River, Kennebec system or other coastal rivers. Cases of upstream movement by some gravid fish in the fall are of particular interest. If such movements involve exploration for potential spawning habitat, then the sudden increase in such habitat following lower dam removals, could lead to the re-establishment of spawning below Milford Dam and the abandonment of spring migrations to the Kennebec system by some gravid females. If shortnose sturgeon begin spawning in the Penobscot River, spring migration rates could be reduced. However, if spawning does not resume in the Penobscot following dam removals, spring migration rates will probably remain un-changed. Additional study will be required following dam removals in the Penobscot River to determine if spawning areas are utilized below Milford Dam and to parse out shifts in regional migration patterns.

2.6 Conclusions

Although spawning was not documented in the Penobscot River, acoustic telemetry observations reinforced the importance of the Kennebec system within the GoM. Without the information on gravid female migrations to the Kennebec system, the lack of documented spawning in the Penobscot River would have led to very different conclusions than were reached during the course of this study. It may have been concluded that without successful spawning, the Penobscot River population was in

serious danger of extirpation. In the case of shortnose sturgeon in the Penobscot River, acoustic telemetry was instrumental in uncovering coastal movements and inter-river exchange of reproductively mature sturgeon to the Kennebec system. Moreover, it appears that shortnose sturgeon populations in the GoM may constitute a larger metapopulation with high rates of exchange between patches or local populations.

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**APPENDIX: HABITAT SUITABILITY FOR SPAWNING SHORTNOSE
STURGEON: BATHYMETRIC ASSESSMENT
UPSTREAM OF VEAZIE DAM**

A.1 Abstract

The possibility of suitable spawning habitat between Veazie Dam and Great Works Dam was investigated with a hydrodynamic model. Bathymetric data was collected in the reach during fall 2011 and a hydrodynamic model was created to investigate shortnose sturgeon spawning habitat suitability. Model results suggest the presence of suitable habitat over a wide range of river discharges below the Great Works Dam. Predicted suitable habitat decreases with increasing river discharge and the distribution of suitable habitat becomes restricted to areas near the river bank. Great Works Dam is slated to be removed prior to the removal of Veazie Dam and shortnose sturgeon will not encounter the structure Great Works Dam after summer 2012. This study provides an assessment of the reach prior to the removal of the dam and will allow post-removal habitat comparison.

A.2 Introduction

The upcoming removal of Veazie Dam and Great Works Dam will restore access to historic shortnose sturgeon habitat in the Penobscot River. Spawning has not yet been documented in the Penobscot (Chapter 2); however, dam removals have the potential to expand habitat available for spawning. In addition, bathymetric data can provide an estimate of suitable habitat (spawning, rearing, etc.) within the reach along with the spatial distribution of that habitat when coupled with a hydrodynamic model capable of

habitat analysis. Within a large river, such as the Penobscot, hydrodynamic models are a useful tool for targeting sampling in likely spawning areas. An assessment of spawning habitat suitability between Veazie Dam and Milford Dam has not been conducted.

This work focuses on the spawning suitability of the reach between Veazie Dam and Great Works Dam. Although Great Works Dam is slated for removal prior to Veazie Dam, this assessment provides a measure of the feasibility of modeling the reach downstream of Milford Dam and an understanding of the habitat that will be available for spawning once the Veazie Dam is removed. In other river systems shortnose sturgeon spawn in the spring as flows decrease from peak discharge and water temperature warms. In the Penobscot River sturgeon are expected to spawn at discharges of 412 cms to 1308 cms (Chapter 1). To assess potential spawning habitat in the reach between Veazie Dam and Great Works Dam bathymetry was collected and a hydrodynamic model constructed and analyzed at discharges typical of spring spawning conditions.

A.3 Methods

Bathymetry between Veazie Dam and Great Works Dam was collected using the same methods as bathymetry surveys in the Bangor Dam reach (Chapter 1). Bathymetric data was post-processed and the river bank defined by appending data points along the entire bank of the reach to the bathymetry file. These data points were then incorporated into a River 2D model as described in Chapter 1. Modeled river discharges were 412 cms, 580 cms, 793 cms, and 1009 cms, and 1308 cms. The river is not tidal in this reach, requiring only one downstream boundary elevation to be modeled for each discharge.

All models were analyzed with the spawning suitability methods described in Chapter 1, which are dependent on water depth and velocity. Combined suitability, both depth and velocity, was calculated for each node in the domain. Once calculated, each node was assigned a suitability ranking which provides a measure of suitable area associated with individual nodes. The sum of all suitable nodal areas is the total weighted useable area (WUA) of the model. This value, WUA, was used to compare the amount of suitable habitat between each modeled discharge. In addition, River 2D allows the display and export of the spatial distribution of habitat suitability.

A.4 Results

Bathymetry was collected on November 8, 2011 at a discharge of 210 cms. The survey was conducted from immediately downstream of Great Works Dam to Ayer's Rips and consisted of 53,396 data points (Figure A.1). The river bank was defined by 2,045 data points with an elevation of 2.0 m.

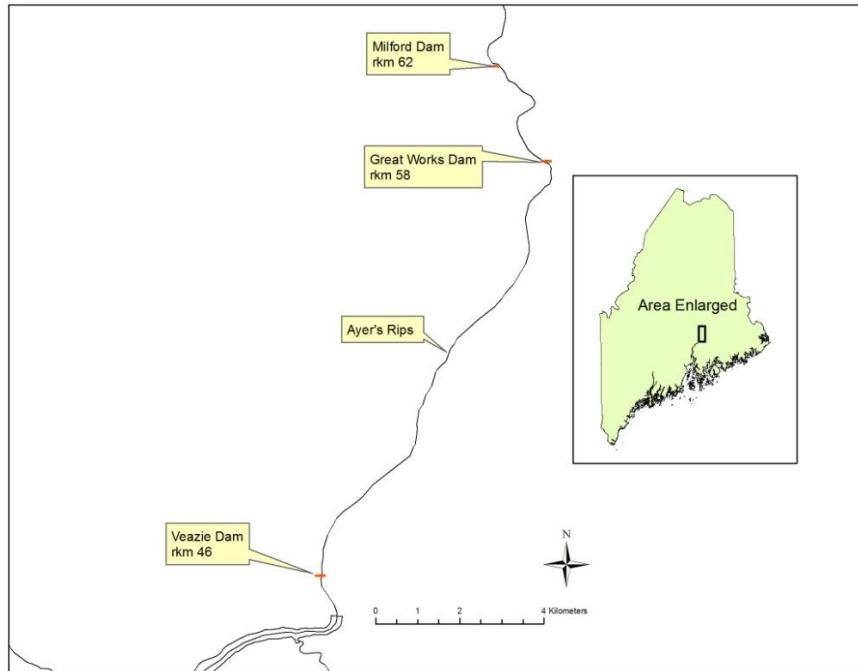


Figure A.1. Study Area. This study took place between Veazie Dam and Great Works Dam on the Penobscot River, Maine. The bathymetric survey conducted in 2011 was between Ayer's Rips and Great Works Dam.

A River 2D bed file was created with the complete dataset and imported into River 2D Mesh (Figure A.2). The initial mesh was constructed with a uniform node spacing of 15 m. The mesh was then smoothed three times and nodes manually added in areas of large elevation changes. The final mesh quality index was 0.2013, well above the recommended 0.15 (Steffler and Blackburn 2002). A River 2D input file was created with this mesh with a downstream boundary of 1.5 m and an inflow discharge of 412 cms. This discharge value was the 5th percentile of observed discharges during the spring spawning windows of 2003 – 2007. The 412 cms model was run to convergence and spawning habitat analyzed. Inflow discharge was then changed to 580 cms, 793 cms, 1009 cms, and 1308 cms. The downstream boundary elevation was increased to 1.6 m, 1.8 m, and 2.0 m for the 793 cms, 1009 cms, and 1308 cms models respectively. Due to the absence of both ADCP calibration points and a USGS gauging station in the reach,

downstream boundary elevations were selected based on the assumption that water depths at the modeled discharges would be deeper than observed depths during the bathymetric survey. All models converged to a stable solution.

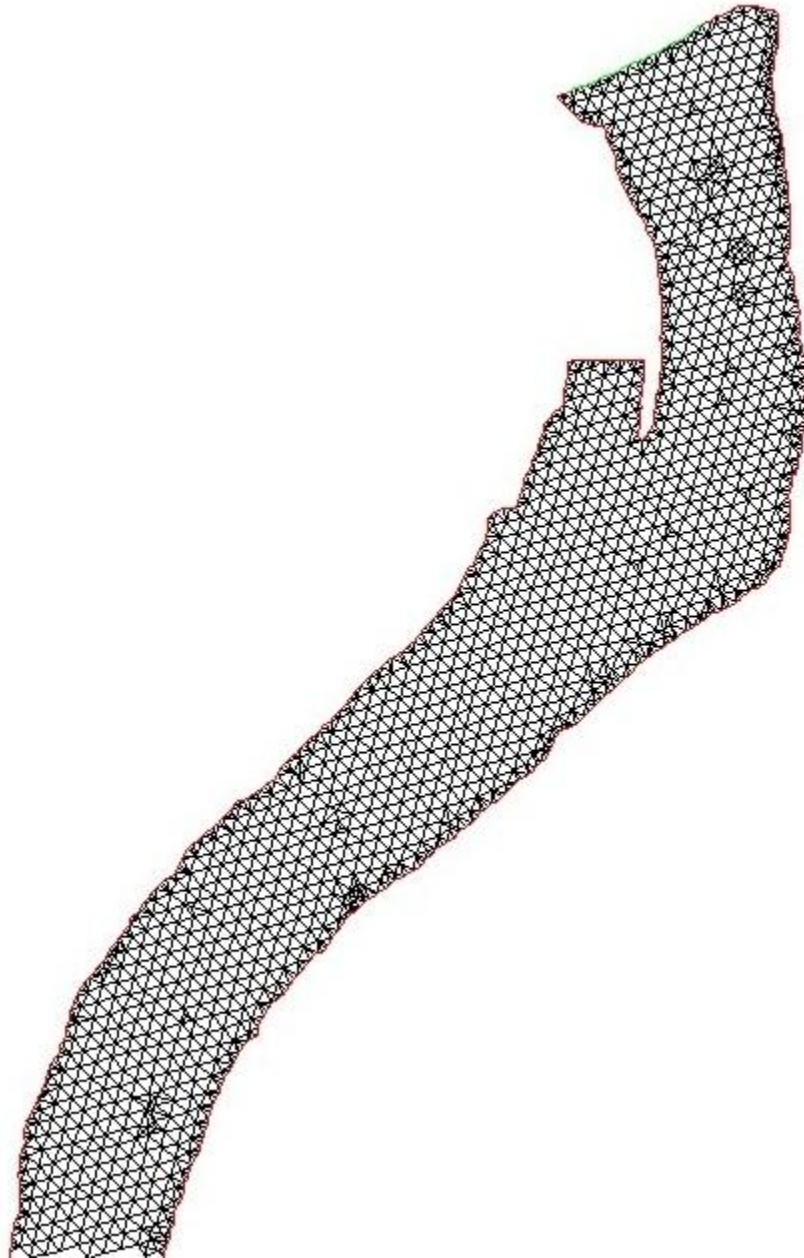


Figure A.2. Excerpt of model mesh. This River 2D mesh of the Penobscot River between Veazie Dam and Great Works Dam was constructed with a node spacing of 15.0 m and is representative of the entire model.

Percent spawning habitat WUA was highest for the 412 cms model and decreased as discharge increased (Figure A.3). Suitable habitat predicted in the models was primarily distributed along the margins of the river where water velocities were slow enough, yet water depth maintained. There are areas directly downstream of the Great Works Dam that were predicted to have suitable habitat at all discharges modeled (Figure A.4). These areas are on the East side of the river and occur near the bank as well as behind the dam.

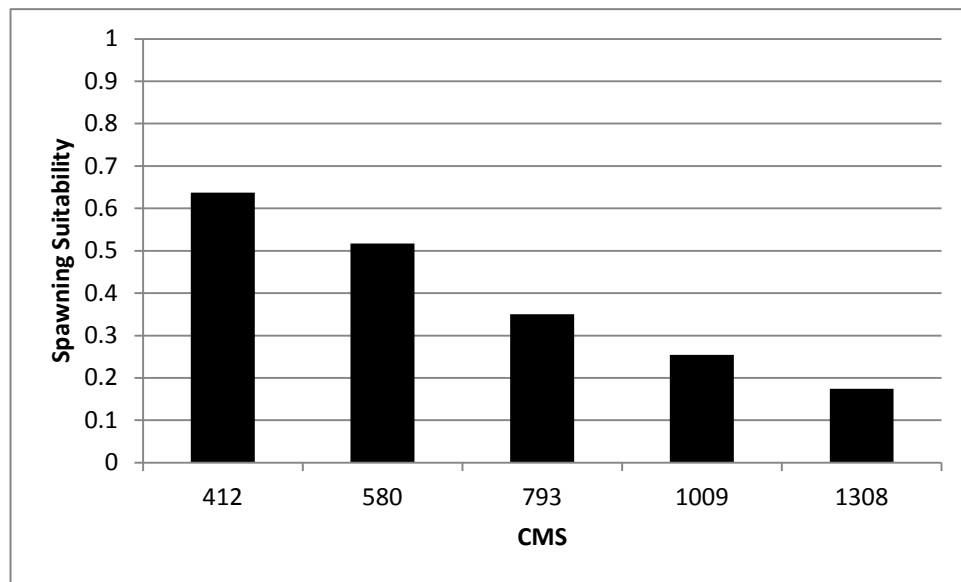


Figure A.3. Percent WUA. The percent weighted usable area for spawning predicted in the reach between Ayer's Rips and Great Works Dam for each discharge modeled. Discharge is indicated as cms.

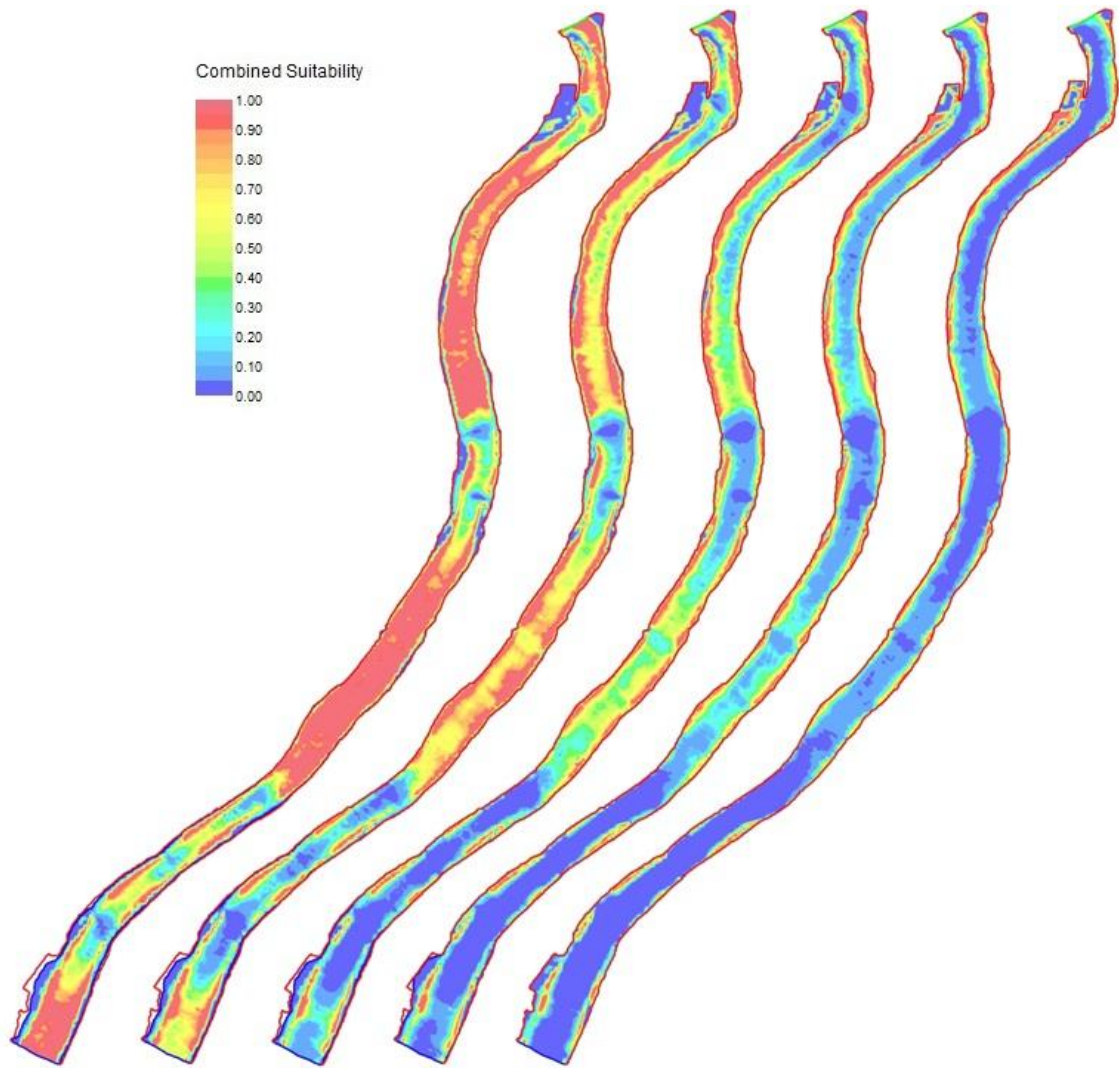


Figure A.4. Spawning suitability distribution. Predicted spawning suitability at each modeled discharge are shown with warmer colors representing areas of higher combined (depth and velocity) suitability. The 412 cms model is on the left, discharge progresses left to right with 1308 cms on the far right. The uppermost boundary is the Great Works dam, the lower boundary is just downstream of the confluence of the Stillwater River and the Penobscot River.

A.5 Discussion

The reach between Veazie Dam and Great Works Dam is characterized by cobble and boulder substrate, shallow water depths, and high water velocities. Suitable spawning habitat is predicted in this reach at all discharges modeled and is distributed

along the margins of the river, especially at higher discharges. This distribution of suitable spawning habitat is similar to the distribution of suitable spawning habitat in the first kilometer downstream of the Veazie Dam (Chapter 1). Additionally, all models predicted suitable spawning habitat downstream of Great Works Dam. If Veazie Dam were to be removed prior to Great Works Dam this area would be expected to host spawning due to the propensity of shortnose sturgeon to spawn directly below the first blockage to upstream movement (Dadswell et al. 1984, Kynard 1997).

However, Great Works Dam will be removed before Veazie Dam and shortnose sturgeon will not encounter the intact structure. Following the removal of Great Works Dam, sturgeon will have access to the base of Milford Dam. Also, the reach between Great Works Dam and Milford dam is quite similar; generally shallow and rocky with high water velocities. Within the Veazie Dam to Great Works Dam reach, model results suggest that suitable spawning habitat should be present along the margins of the entire reach. While the Great Works Dam to Milford Dam reach has not been surveyed or modeled, it is likely that suitable spawning habitat is distributed along the margins of the reach and immediately downstream of Milford Dam.

Models in the Veazie Dam to Great Works Dam reach represent an initial assessment of spawning habitat. Bathymetry surveys were conducted at a discharge of 210 cms. As such, many shallow, rocky portions of the reach could not be measured and were therefore interpolated in the model. Specifically, eight long, shallow runs were surveyed with a single pass. These runs are represented in the model as uniform basins; depth is interpolated from the transect to the bank and nearest upstream and downstream data points (Figure A.5). While these areas of the model suffer from a lack of data, they

occur in locations that are not likely to host shortnose sturgeon spawning, due to shallow depths and high water velocities, and are assumed to have a negligible effect on spawning habitat results (Kynard 1997, Crance 1986).

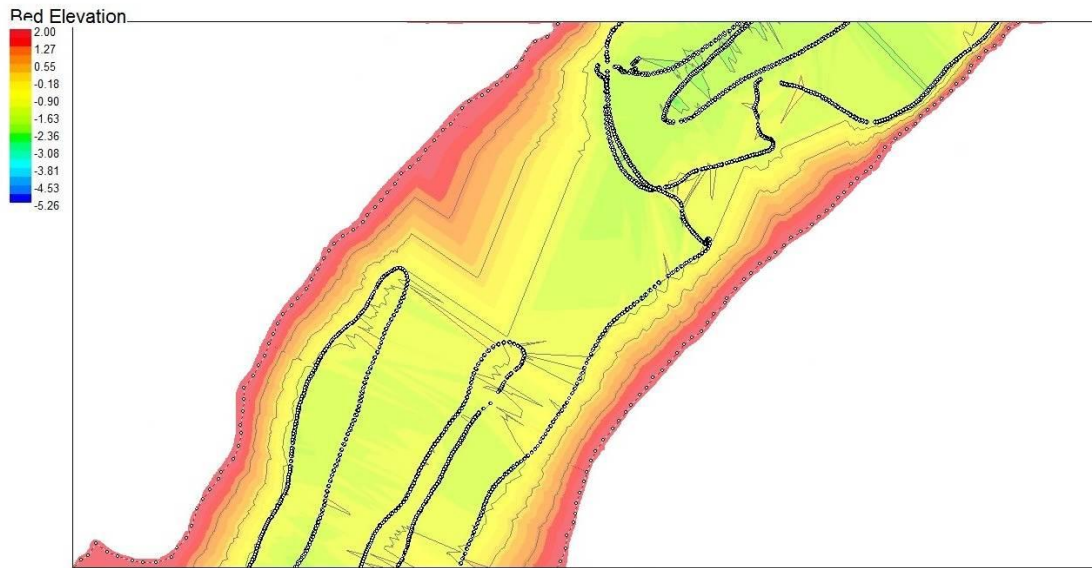


Figure A.5. Modeled depth with sparse bathymetry. A representative shallow run of the Penobscot River between Veazie Dam and Great Works Dam that was not surveyed with multiple transects and transects are shown as black dots. Depth contours are 1.0 m.

One area that was not extensively surveyed and may influence results is the tailrace of Great Works Dam. Due to the low discharge during bathymetry collection there were areas of the tailrace that were not surveyed (Figure A.6). Current spawning habitat predictions suggest that suitable spawning habitat is present along the East side of the tailrace at all discharges modeled (Figure A.7). However, this is the area lacking survey data and an additional survey is needed to fill in data gaps.



Figure A.6. Bathymetry at Great Works Dam. This graphic shows bathymetry transects at the Great Works Dam. At the time of data collection the areas not surveyed were in-accessible.

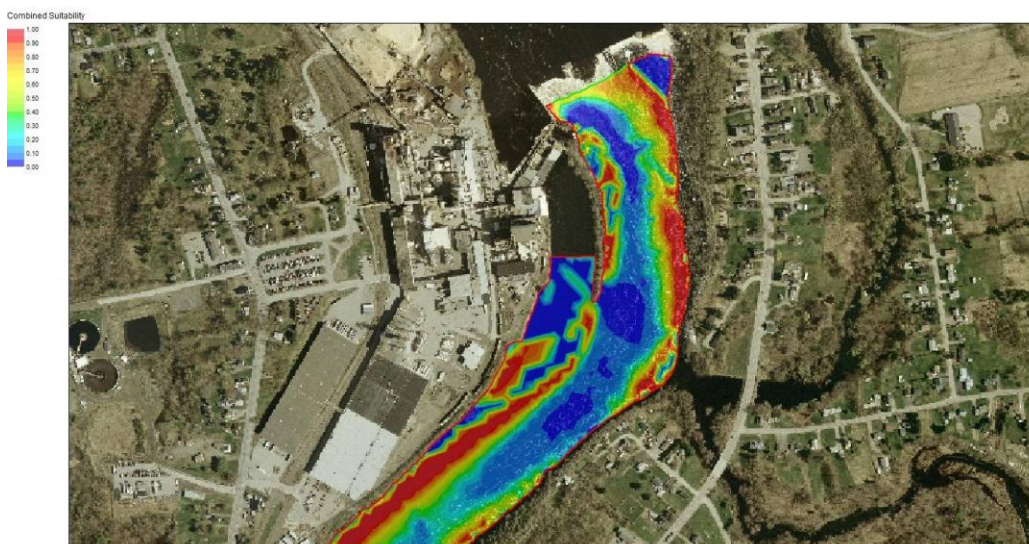


Figure A.7. Great Works Dam tailrace spawning suitability. Shown is the predicted spawning suitability below Great Works Dam. Warmer colors are areas of higher predicted suitability. The area on the East side of the river is predicted to be suitable at each discharge. However, there is a lack of bathymetric data in these areas and should be a priority for future surveys.

River flow patterns at the Great Works Dam change in the tailrace based on dam operation, particularly when water is spilled over localized portions of the structure. Following the dam's removal it will be interesting to examine how the distribution of suitable spawning habitat in the former tailrace changes. Localized discharge over the dam was accounted for in the model by restricting the inflow boundary to a portion of the river's cross section at the upstream boundary. Suitable spawning habitat on the East side of the tailrace is directly influenced by the restricted inflow boundary and reduced water velocities associated with the localized discharge of the inflow boundary. Without the dam in place water will flow much more evenly through the former tailrace and will probably alter spawning habitat distribution.

Additional data should be collected to calibrate and validate the model. Depth calibration points were not collected within this reach. As such, the downstream boundaries were set based on measured depths during the survey with the assumption that depths at modeled flows would be slightly deeper than observed values. While this is a potential source of error, it is probably minimal within this reach. Also, data should be collected to form a more accurate representation of river conditions at representative spring discharges. Specifically, bathymetry surveys should be conducted at higher discharges in order to survey areas that were in-accessible during the 2011 survey. Also, surveys should target areas of highly variable bathymetry throughout the reach that may have been in-completely surveyed instead of uniform regions of the river bed. Nonetheless, it appears that suitable spawning habitat is present below the Great Works Dam.

Although Great Works Dam will be removed before sturgeon have access to the reach, this remains an informative exercise. If bathymetric data is collected between Great Works Dam and Milford Dam, it can be combined with the Veazie Dam to Great Works Dam bathymetry to construct a model to predict likely locations of spawning in the restored reach before the removal of Veazie Dam. This information could be instructive to future spawning sampling in the Milford Dam tailrace if the proper data are collected and analyzed.

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Matthew T. Wegener was born in Farmington, New Mexico to his parents, Emily and Barney Wegener. Matthew grew up in the north west corner of New Mexico, hunting and fishing at all opportunities. Following graduation from Bloomfield High School, Matthew moved to Missoula, Montana to pursue a degree in Wildlife Biology. Matthew graduated with a Bachelor's of Science in Wildlife Biology from the University of Montana in May, 2007. He is a candidate for the Master of Science degree in Marine Biology from the University of Maine in August, 2012.